

Looking beyond the mean:
Drivers of variability in postfire stand development of Rocky Mountain conifers

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Drivers of variability in postfire stand development of Rocky Mountain conifers

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Abstract

High-severity, infrequent fires in forests shape landscape mosaics of stand age and structure for decades to centuries, and forest structure can vary substantially even among same-aged stands. This variability among stand structures can affect landscape-scale carbon and nitrogen cycling, wildlife habitat availability, and vulnerability to subsequent disturbances. We used an individual-based forest process model (iLand) to ask: *Over 300 years of postfire stand development, how does variation in biotic versus abiotic conditions influence among-stand structural variability for four conifer species widespread in western North America?* We parameterized iLand for lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) in Greater Yellowstone (USA). Simulations were initialized with field data on regeneration following stand-replacing fires, and stand development was simulated under historical climatic conditions without further disturbance. Stand structure was characterized by stand density and basal area. Stands became more similar in structure as time since fire increased. Basal area converged more rapidly among stands than among-stand tree density for Douglas-fir and lodgepole pine, but not for subalpine fir and Engelmann spruce. For all species, regeneration-driven variation in stand density persisted for at least 80 years postfire, and for lodgepole pine, early regeneration densities dictated among-stand variation for up to 270 years. The relative importance of abiotic and biotic drivers of stand structural variability differed between density and basal area and among species due to differential species traits, growth rates, and sensitivity to intraspecific competition versus abiotic conditions. Understanding dynamics of postfire stand

development is increasingly important for anticipating future landscape patterns as fire activity increases.

Keywords: Stand structural variability; forest development; process-based modeling; Greater Yellowstone Ecosystem; wildfire

Introduction

Large, high-severity, infrequent disturbances such as fires can shape landscape patterns of forest age, structure, and species composition for decades to centuries (Foster et al. 1998). Warming climate and concomitant increases in fire activity will likely reset forest succession across larger expanses of the western United States (Westerling et al. 2006, Abatzoglou and Williams 2016, Westerling 2016). Therefore, understanding how stands develop after fire is critical for anticipating future forest landscapes. This is particularly important in the Northern Rocky Mountains (USA), where decadal area burned increased 889% from the 1970s to the early 2000s (Westerling 2016) and 34% of area burned across all forest types is stand-replacing fire (Harvey et al. 2016a).

Among-stand variation in forest structure over stand development has received surprisingly little attention in studies of postfire stand trajectories (but see Kashian et al. 2005a, 2005b). Structure and function can vary considerably among stands of the same age (e.g., Turner 2010), with substantial implications for carbon pools and fluxes (Litton et al. 2004, Turner et al. 2004, Bradford et al. 2008, Kashian et al. 2013), nitrogen pools and fluxes (Smithwick et al. 2009a, 2009b, Turner et al. 2009), wildlife habitat (Tews et al. 2004), and vulnerability to subsequent disturbances (Bebi et al. 2003, Seidl et al. 2016a). Due to high variation in stand structure and ecosystem function following fire, simple descriptions of mean conditions within these forests might overlook important information about the ecological dynamics of a landscape (Fraterrigo and Rusak 2008).

Initially distinct post-disturbance stands may converge over time due to competition and environmental constraints, or follow distinct trajectories if the effects of initial post-

disturbance regeneration and environmental heterogeneity persist over time (Glenn-Lewin and van der Maarel 1992, Walker and del Moral 2003). Postfire stand development pathways differ among species based on their fire adaptations, growth rates, and tolerances. For example, species that exhibit serotiny depend on a canopy seedbank that must be released by an environmental trigger such as fire. Serotinous species [e.g., lodgepole pine (*Pinus contorta* var. *latifolia*), jack pine (*Pinus banksiana*)] can recruit in abundance following stand-replacing fire (Turner et al. 2004, Buma et al. 2013, Pinno et al. 2013, Edwards et al. 2015]). In contrast, others species must disperse into recently burned areas (Baker 2009). In the Northern Rocky Mountains, postfire lodgepole pine densities vary widely as a result of broad-scale gradients in prefire serotiny (Tinker et al. 1994, Turner et al. 1997, Schoennagel et al. 2003). Variation in early regeneration densities will result in different levels of competition for light and other resources in postfire stands. Abiotic heterogeneity may also be an important driver of variation in postfire stand development, as high-severity fire occurs in forests that span a broad range of climatic and topographic conditions (Turner and Romme 1994, Harvey et al. 2016a).

Dynamics of postfire stand development will unfold over long periods of time and under changing climate, and models that can project variation in future stand structures are needed to explore these long-term trajectories and inform possible forest management practices. Models built on statistical relationships between environmental drivers and tree responses (i.e., empirical models) play an important role in forest management and form the basis for the development of more complex models based on mechanistic understanding of forest processes (Korzukhin et al. 1996). However, empirical models may fail to predict

stand structures and forest landscapes under changing environmental drivers, whereas process-based models can improve projections of future forest conditions (Korzukhin et al. 1996, Cuddington et al. 2013, Gustafson 2013, Reyer et al. 2015). Modeling ecological processes and variables at scales appropriate to phenomena, such as competition for resources at the individual-tree level, also allows broader-scale patterns to emerge from finer-scale interactions (Grimm et al. 2017, Scholes 2017).

We adapted and parameterized iLand, a process-based forest simulation model (Seidl et al. 2012) for four widespread conifer species in the Greater Yellowstone Ecosystem: Lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). iLand has been demonstrated to work well in forested ecosystems in the Pacific Northwest (Seidl et al. 2012, 2014b) and in Europe (Seidl et al. 2014a, Silva Pedro et al. 2015, Thom et al. 2017), as well as for some conifer species in Yellowstone (Hansen et al. 2018). Because iLand had not previously been used for our focal species in the Greater Yellowstone Ecosystem, we first evaluated model performance using independent data for the region. We then conducted a simulation experiment to explore controls on long-term stand development of postfire forests. We asked: *Over 300 years of postfire stand development, how does variation in biotic versus abiotic conditions influence among-stand structural variability for four conifer species widespread in western North America?* We expected variation in early regeneration densities to drive structural variability among young stands and variation in abiotic drivers to become increasingly important as stands aged. We further expected early regeneration densities to influence stand structural variability of lodgepole pine for a longer period of time

than other conifers, due to its wider range of initial stem densities resulting from variation in prefire serotiny.

Methods

Study area

The Greater Yellowstone Ecosystem (GYE) in the Northern Rocky Mountains of the United States comprises 89,000 km² (YNP 2017) primarily in northwest Wyoming, and also in southeast Idaho and southwest Montana. The majority of the GYE is federally managed land, anchored by Yellowstone and Grand Teton National Parks and adjacent national forests, and natural processes such as disturbance and regeneration occur with minimal intervention across large areas within this relatively intact forested landscape. Forests in the GYE span a broad elevation gradient (1,800 to 3,050 m) and include lower-elevation montane forests dominated by interior Douglas-fir, mid-elevation subalpine forests dominated by lodgepole pine, and higher-elevation subalpine forests dominated by Engelmann spruce and subalpine fir (Despain 1990, Knight et al. 2014). Climate is warmer and drier at lower elevations, and cooler and wetter at higher elevations (Figure 1). Soils in the central area of Greater Yellowstone are largely derived from underlying rhyolitic or andesitic bedrock (Rodman et al. 1996). Rhyolite-derived soils, which cover most of Yellowstone's lodgepole pine-dominated central plateau, are coarser and less fertile than andesite-derived soils (Despain 1990, Whitlock 1993).

Forests in the GYE have been shaped by historical fire regimes. Subalpine forests in this region experienced infrequent (100-300 year fire rotation), high-severity (i.e., stand-

replacing) fires throughout the Holocene (Romme and Despain 1989, Millspaugh et al. 2004, Schoennagel et al. 2004, Whitlock et al. 2008, Higuera et al. 2011). Fire regimes in low-elevation Douglas-fir forests are typically characterized as mixed severity (Baker 2009), but stand-replacing fires can occur in all forest types (Baker et al. 2007, Harvey et al. 2016a). Postfire regeneration densities following stand-replacing fire are extremely variable (Table 1) based on prefire stand conditions, local burn severity, and the spatial pattern of fires, which determine distances to seed sources (Turner et al. 1997, 1999). For example, regenerating lodgepole pine stands ranged from 0 to > 500,000 stems ha⁻¹ 11 years following stand-replacing fire (Turner et al. 2004). High-severity fire behavior in this region is primarily weather-driven (e.g., drought, wind; Schoennagel et al. 2004, Higuera et al. 2011). Fire frequency, fire season length, and area burned have increased in recent decades (Westerling 2016), a trend that is projected to continue over the coming century as the climate becomes warmer and drier (Westerling et al. 2011).

Model overview and evaluation

We simulated stand development using the individual-based forest landscape and disturbance model iLand (Seidl et al. 2012), which integrates species-specific responses to environmental drivers such as light availability, temperature, precipitation, soil moisture, and nutrient levels. These environmental drivers limit seedling cohort establishment (2-m spatial resolution) and modify sapling cohort growth and survival. Trees > 4 m in height are represented as individuals (2-m spatial resolution) in their responses to resource availability. Limitations to physiological processes (e.g., temperature and water limitation) are considered

at a daily time step, while stand structure is updated annually. Processes such as seed dispersal and competition for light are spatially explicit. Light availability for an individual tree is attenuated based on the heights and crown characteristics of neighboring trees. The growth allocation of individual trees to height and diameter responds dynamically to light competition within a species-specific range. In the absence of disturbance, variation in tree sizes and forest structure within stands (i.e., 100 × 100 m grid cells of homogeneous climate and soil conditions) emerges from these fine-scale tree-level dynamics, while among-stand variability is also driven by differences in environmental conditions between stands (Seidl et al. 2012). Extensive model documentation is available at <http://iland.boku.ac.at/> (Seidl and Rammer 2018).

We parameterized iLand for the four dominant conifer species in the Greater Yellowstone Ecosystem (see Appendices). Most species-specific traits and parameters were sourced from peer-reviewed literature and government reports, and a few parameters (e.g., height-to-diameter ratios, aging) were fit or iteratively derived by simulating stand development of initial conditions (see Seidl et al. 2012 and Seidl and Rammer 2018).

We evaluated simulated structural trajectories and variability over time against field data on stand density, basal area, quadratic mean diameter (QMD), and mean height in monospecific stands. Model runs were initialized using species-specific field data recorded in postfire stands in the GYE following stand-replacing fires that burned between 1988 and 2003 (Table 1, Figure 2). Individual trees (densities, diameters, and heights), and the number and height of sapling and seedling cohorts were initialized for each simulated stand (Donato et al. 2016, Harvey et al. 2016b, Turner et al. 2016). Because our interest here was in long-

term stand development once early postfire establishment had occurred, we began simulations with stands that were 10-25 years postfire (but see Hansen et al. 2018 for simulations of early postfire establishment).

For each postfire stand, we extracted historical (1980-2015) climate drivers (temperature, vapor pressure deficit, precipitation, and radiation) from Daymet Version 3 (1-km gridded daily climate data; Thornton et al. 2017) and soil depth and texture from CONUS-SOIL (1-km spatial resolution; Miller and White 1998) using geographic coordinates of postfire field plot locations (Figure 2). Lodgepole pine plots were widely distributed across Yellowstone National Park. However, some field plots for Douglas-fir, Engelmann spruce, and subalpine fir stands were separated by less than 1 km, resulting in replicated climate conditions, and higher-elevation Engelmann spruce-subalpine fir climates were underrepresented. To adequately simulate expected ranges of abiotic variability for each species, we extracted additional climate and soil conditions in the GYE based on field-verified forest type (see Figures 1-2; Simard et al. 2012). We assigned soil nutrient availability based on relative fertility of soil parent material (andesite, rhyolite, or lacustrine sediments) recorded in field data (when available) or by species (e.g., high-elevation Engelmann spruce and subalpine fir are associated with andesite parent material in this region; Despain 1990, Knight et al. 2014).

We simulated development of monospecific 1-ha stands for 300 years with no additional disturbance under historical climate conditions. Climate year was randomly drawn with replacement from 1980 to 2015. Initial trees and saplings within a stand were the only seed source for subsequent tree recruitment. Stands were simulated using a torus, in which

influences that leave one edge of the stand (e.g., shading of neighboring trees) enter the opposite edge of the stand, eliminating edge effects.

We evaluated how well the model simulated variation in stand development trajectories by comparing stand-level live tree densities, basal areas, QMDs, and mean heights with independent field observations (Kashian et al. 2005a, 2013, Simard et al. 2011, Donato et al. 2013a, Griffin et al. 2013) and data from the Forest Inventory and Analysis (FIA) Database (USDA Forest Service 2016). Field observations included stands dominated by lodgepole pine or Douglas-fir that were either undisturbed or had recently experienced bark beetle disturbance (red stage). In the latter, standing dead trees were treated as live trees for the purpose of comparison. The FIA stands for Douglas-fir, Engelmann spruce, and subalpine fir were selected from unreplicated (inventory year 2000) stands on federally owned land and dominated ($> 75\%$ of tree density) by the focal species. All stand ages in comparison data were plotted as time since stand-replacing fire. For consistency with field data, metrics of stand structure were calculated for trees > 4 cm diameter at breast height (DBH).

Additional evaluations of mixed-species stands and a comparison with the forest growth model Forest Vegetation Simulator (FVS; Dixon 2002, Keyser and Dixon 2008) assessed successional trajectories, species composition and stand structure in late-seral stages in different forest types, and stand-level responses to variation in initial stem densities and environmental conditions (see Appendices).

Simulation experiment

We used postfire regeneration, climate, and soil conditions from the stands used for evaluation in a 2-by-2 factorial simulation experiment (Table 2) to assess the influence of variation in biotic versus abiotic drivers of among-stand structural variability. All stands were either simulated with observed variation in postfire regeneration and environmental conditions or with no among-stand variation. Because our aim was to separate effects of differing drivers and because climatic conditions were correlated with early regeneration densities, abiotic (climate plus soil depth and texture) conditions were randomly assigned to early postfire regeneration densities by species. Soil relative fertility was held constant by species to control for variation in available field data on soil substrate, and simulated stands were assigned a fertility value based on rhyolite parent material for lodgepole pine and andesite parent material for Douglas-fir, Engelmann spruce, and subalpine fir.

Simulated stands represented a wide range of biotic and abiotic conditions (Table 1, Figure 1). Initial stem densities for each species varied from two to four orders of magnitude. Among stands of all species and over the 36-year climate period, mean annual temperature ranged from -1.3 to 4.3 °C, and mean annual precipitation from 444 to 1,400 mm. All species spanned a mean annual temperature range of > 2.5 °C, with Engelmann spruce stands covering the widest range (4.4 °C). The minimum range of mean annual precipitation among stands of a single species was 240 mm, with the widest gradient exhibited among lodgepole pine stands (771 mm). Soils ranged from 30-71% sand content, with lodgepole pine stands having the coarsest soil on average (i.e., highest mean and median sand content).

We simulated four scenarios of variation in abiotic and biotic drivers of stand structural variability (*All vary*, *Abiotic varies*, *Regeneration varies*, *None vary*; Table 2). A representative abiotic and biotic stand was derived for each species based on the central tendency of observed drivers (i.e., median soil depth and texture, climate period with median vapor pressure deficit, stand with median postfire regeneration stem density; Table 1, Figure 1). For scenarios with no abiotic or biotic among-stand variation, the respective representative stand conditions were assigned to all simulated stands for a given species. Climate varied interannually in all scenarios. For each scenario, we simulated 20 replicates for 300 years postfire with no disturbance following the methods described above in model evaluation.

Model outputs and analysis

Stand structure for each species was characterized using two metrics, stand density and stand basal area. Both metrics were calculated each year for trees > 4 m in height. The coefficient of variation (CV) was used to quantify variation in structure among stands of the same species and age (as in Kashian et al. 2005a, 2005b). As a relative estimate of variance, the CV enables comparisons among datasets with different means (Fraterrigo and Rusak 2008).

For each species and scenario (Table 2), mean stand density, mean stand basal area, and mean CV (among the $n = 20$ replicates) were calculated for each year. We first summarized general trends in among-stand variation in structural trajectories of same-aged stands for the *All vary* scenario, in which both abiotic and biotic conditions varied among

stands, as a baseline for comparison with the *Abiotic varies* and *Regeneration varies* scenarios. We assessed differences in how stand structure converged among species based on when CV declined to 100% and when mean stand density peaked. We next compared trends among scenarios for each species. For *Abiotic varies* and *Regeneration varies* scenarios, the point of intersection of mean CVs and the overlap of CV ranges (minimum to maximum CV across the 20 replicates) were used to characterize time periods at which abiotic versus biotic drivers were more important in influencing among-stand variation. Trends among species were compared based on time since fire in years. R statistical software (R Core Team 2017) was used for all analyses of model outputs.

Results

Model evaluation

Simulated stand densities in iLand for all four species fell within observed ranges of field data over 300 years of stand development, and variation in stand density and basal area corresponded well to observations over time since fire (Figure 3; for QMDs and mean heights see Appendix B, Figure B1). At 300 years postfire, Douglas-fir densities (trees > 4 cm DBH) ranged from 110-602 trees ha⁻¹ (mean 268 trees ha⁻¹), lodgepole pine from 705-1,693 trees ha⁻¹ (mean 927 trees ha⁻¹), subalpine fir from 357-937 trees ha⁻¹ (mean 623 trees ha⁻¹), and Engelmann spruce from 330-917 trees ha⁻¹ (mean 532 trees ha⁻¹). Simulated basal areas also were within observed ranges for Douglas-fir, lodgepole pine, and Engelmann spruce throughout stand development; however, field observations for older (> 150-year-old) subalpine fir stands showed a decline in basal area that was not captured in simulated stands

(Figure 3f). Simulated stands did not always achieve maximum or minimum values observed in the field. Across all species, the range of iLand simulations encompassed 64% of field observations of stand density ($n = 187$) and 67% of field observations of basal area ($n = 187$).

Additional iLand evaluations were consistent with expectations based on field data and model comparison with the Forest Vegetation Simulator. In mixed-species evaluations, iLand produced expected forest types, and late-seral stand structure and composition overlapped with published data (Appendix B, Figures B4-B7; Binkley et al. 2003, Kashian et al. 2005b, Donato et al. 2013b). High-elevation spruce-fir stands exhibited anticipated successional trajectories, with subalpine fir basal area declining in older stands as longer-lived spruce increased in dominance (Aplet et al. 1988, 1989). In model comparison evaluations, lodgepole pine and Douglas-fir stand structures followed similar trajectories in both iLand and FVS for at least 50 years postfire (Appendix B, Figures B8 and B9).

Variation in among-stand structural trajectories (All vary scenario)

When stands varied both in their early postfire densities and their abiotic conditions (*All vary scenario*), among-stand CVs for stand density and basal area were highest at or near the beginning of the simulation. Stands eventually converged in density (Figure 4) and in basal area (Figure 5), but the timing of convergence differed among species. Stand density converged most rapidly for lodgepole pine (mean among-stand density CV declined below 100% by 43 years postfire), followed by Douglas-fir (48 years), subalpine fir (71 years), and Engelmann spruce (81 years; Figure 4). Mean stand density (trees > 4 m height) also peaked earlier in stand development for both lodgepole pine (2,960 trees ha⁻¹ at 31 years postfire)

and Douglas-fir (468 trees ha⁻¹ at 37 years postfire) compared to subalpine fir and Engelmann spruce (817 trees ha⁻¹ and 1,005 trees ha⁻¹ at 149 and 143 years postfire, respectively). At peak stand density, among-stand variation was greater for Douglas-fir and lodgepole pine (mean CV = 112% for Douglas-fir and 108% for lodgepole pine) than for subalpine fir (mean CV = 32%) or Engelmann spruce (mean CV = 24%). By 300 years postfire, among-stand variability in density had declined to $\leq 45\%$ mean CV for all species (Table 3).

Basal area converged more rapidly than stand density for Douglas-fir and lodgepole pine, with mean among-stand basal area CV falling below 100% by 30 and 25 years postfire, respectively (Figure 5). However, basal area converged more slowly than stand density for subalpine fir and Engelmann spruce (mean CV declined below 100% by 93 and 90 years postfire, respectively). By 300 years postfire, among-stand variability in basal area had declined to a mean CV of $\leq 23\%$ for all species (Table 3).

Influence of biotic versus abiotic conditions on stand structural variability

Trajectories of mean tree density were similar over time across the four scenarios (Figure 4a-d), but trajectories of among-stand variation in density differed among scenarios and species (Figure 4e-h). Early in stand development, mean CVs for stand density were similar when early regeneration densities and abiotic conditions both varied (*All vary*) and when only regeneration densities varied (*Regeneration varies*), but mean CV was much lower when only abiotic conditions varied (*Abiotic varies*). When only early regeneration densities varied, mean CV declined over time as stand density converged, eventually reaching a value lower than the *All vary* scenario. In contrast, when only abiotic conditions

varied, mean CV was initially lower but increased or persisted at a higher value over time. By 300 years postfire, *Abiotic varies* and *All vary* scenarios had similar mean CVs, both of which were greater than the mean CV for *Regeneration varies* (Table 3).

For all species, biotic drivers of among-stand variation in density were most important early in stand development (when *Regeneration varies* scenarios had the highest mean CV), and abiotic drivers were most important later in stand development (when *Abiotic varies* scenarios had the highest mean CV). Between 95 and 217 years after fire, depending on the species, the mean CV when early regeneration densities varied (*Regeneration varies*) was equal to the mean CV when abiotic conditions varied (*Abiotic varies*; point of intersection in Figure 6i-j). Additionally, when considering the full range of CVs across all $n = 20$ replicates per scenario, there was a time period during stand development when CVs in *Abiotic varies* and *Regeneration varies* scenarios overlapped (Table 3, Figure 6). Species differed in both the timing of the point of intersection as well as the timing and duration of overlap.

Variation in early postfire regeneration influenced among-stand variability in lodgepole pine density for a longer period of time than other species. Lodgepole pine *Abiotic* and *Regeneration varies* scenarios intersected at 217 years postfire (Figure 6c). The point of intersection was earliest for subalpine fir stands (95 years postfire; Figure 6e), followed by Engelmann spruce (153 years postfire; Figure 6g) and Douglas-fir (175 years postfire; Figure 6a). Lodgepole pine *Abiotic* and *Regeneration varies* scenarios also had the latest onset (188 years postfire) and ending year (272 years postfire) of overlap in CV ranges, whereas

Engelmann spruce scenarios had the longest duration of overlap (136 years, from 104-240 years postfire; Table 3, Figure 6i).

Mean basal area also followed similar trajectories among all four scenarios (Figure 5a-d), whereas among-stand variation in basal area differed among scenarios and species (Figure 5e-h). In general, mean among-stand basal area variability behaved similarly to mean among-stand density variability over time for each of the four scenarios. Among-stand variation was initially high when only early regeneration densities varied (*Regeneration varies*) or when both regeneration and abiotic conditions varied (*All vary*), but mean CV declined over time. When only abiotic conditions varied (*Abiotic varies*), among-stand variation was initially lower. However, the *Abiotic varies* mean CV equaled (point of intersection) and then surpassed the *Regeneration varies* mean CV over time.

The relative importance of abiotic and biotic drivers of variation differed between basal area and density for a given species. For example, the point of intersection of mean CVs in *Abiotic* and *Regeneration varies* scenarios was earlier for basal area compared to stand density for all species except subalpine fir (Table 3, Figure 6i-j). Lodgepole pine had the earliest point of intersection (67 years postfire; Figure 6d), and mean CVs for subalpine fir (Figure 6f), Douglas-fir (Figure 6b), and Engelmann spruce (Figure 6h) intersected at similar times in stand development (124, 128, and 136 years postfire, respectively). For all species other than Douglas-fir, the duration of overlap in CV ranges between *Abiotic* and *Regeneration varies* scenarios was shorter for basal area and ended earlier compared to density (Table 3, Figure 6i-j). The ranges of Douglas-fir basal area CVs overlapped until the end of the simulation (300 years postfire).

Discussion

Here we show that variation in early postfire regeneration densities affects stand structural trajectories for decades to centuries for four widespread conifer species. Variation in early regeneration densities was particularly important in shaping long-term patterns of lodgepole pine stand densities. Among-stand structural variability was highest in young stands for all species, and stand structures converged with time since fire. Stand density converged more rapidly than basal area (a proxy for stand function) for Douglas-fir and lodgepole pine, but not for subalpine fir and Engelmann spruce. Differential responses among species correspond to variation in life history traits, growth rates, and sensitivity to intraspecific competition versus abiotic conditions. This study highlights the importance of understanding variability in early postfire regeneration and in young stand structures to anticipate future landscape patterns in ecosystems characterized by high-severity, infrequent disturbance regimes.

Variation and convergence in stand structural trajectories

Convergence of simulated stand density when both abiotic conditions and early regeneration varied (*All vary* scenarios) is consistent with postfire chronosequence studies in this region (Kashian et al. 2005a, 2005b). Convergence occurs when initially dense stands undergo self-thinning as individual trees outcompete their neighbors (Peet 1992), while establishment continues in sparser stands where light is available at the forest floor (Kashian et al. 2005b, Turner et al. 2016). Simultaneous self-thinning in some stands and infilling in

others was evident early in simulations of both lodgepole pine and Douglas-fir. In field chronosequences, rapid declines in stand density (until 50 or 100 years postfire) and convergence have also been documented (Kashian et al. 2005b). In contrast, prolonged time to convergence and self-thinning in simulated subalpine fir and Engelmann spruce stands may be related to species' slower initial growth during seedling and sapling stages (Oosting and Reed 1952, LeBarron and Jemison 1953).

Past studies of lodgepole pine stand development in the GYE indicate that stand function converges more rapidly than structure (Kashian et al. 2005a, 2013, Turner et al. 2016), but this was not observed for all species in our simulations. More rapid convergence of function than structure would be consistent with earlier convergence of stand basal area (as a proxy for function) compared to density. Trees in sparser stands may exhibit a compensatory growth response to lower densities (e.g., Copenhaver and Tinker 2014) and therefore tend toward similar basal area as denser stands. However, more shade-tolerant species such as subalpine fir and Engelmann spruce (Oosting and Reed 1952, Alexander 1987) may continue to establish for decades post-disturbance (Veblen 1986, Aplet et al. 1988), enabling earlier convergence in stand density than basal area.

Influence of biotic versus abiotic conditions on stand structural variability

Variation in early postfire regeneration densities dictated stand structural variability for 60 to 188 years, depending on the species (based on the onset of overlap of CV ranges). Over time, stands shifted from competition-driven convergence to environment-driven divergence, in which variability among stands was maintained or increased. This supports

our hypothesis that variation in regeneration densities (i.e., biotic conditions) would drive variability among young stands, with variation in abiotic drivers becoming increasingly important as stands aged. However, the long-lasting influence of early postfire regeneration is striking given the wide range of abiotic conditions. As fire frequency is likely to increase in the future (Westerling et al. 2011), the influence of variation in tree regeneration is also likely to increase relative to the effect of abiotic variation.

Our hypothesis that regeneration would influence stand structural variability of lodgepole pine for a longer period of time than other conifers was supported for among-stand density, highlighting the importance of species life history traits. Traits that favor abundant and rapid initial regeneration after fire, such as high prefire serotiny in lodgepole pine, can have long-lasting effects on stand densities (Mason 1915, Kashian et al. 2005b). Lodgepole pine also regenerates non-serotinely, but shading from an initial cohort may suppress subsequent regeneration and seedling growth (Lotan and Perry 1983, Knight et al. 2014). Given smaller ranges of early postfire densities and prolonged periods of establishment and growth in the understory, species such as subalpine fir and Engelmann spruce may more rapidly overcome initial variation in regeneration. Of the three solely wind-dispersed species, subalpine fir is generally characterized as the most shade-tolerant and as a relatively prolific and regular seeder (Oosting and Reed 1952, Alexander 1987). Consistent with these traits, biotic variation had the shortest influence on subalpine fir stand densities compared to Douglas-fir and Engelmann spruce.

In contrast, our hypothesis that regeneration would have a prolonged influence on lodgepole pine compared to other species was not supported for among-stand basal area.

Differential growth rates and their sensitivity to environmental drivers and competition may explain differences among species. Lodgepole pine is relatively faster growing at young ages and radial growth increment is highly sensitive to crowding (Wykoff 1990, Veblen et al. 1991, Buechling et al. 2017), resulting in accelerated growth of individual trees in sparser stands (Copenhaver and Tinker 2014). Tree growth may also be enhanced given moderate annual precipitation (in the range of 600 to 900 mm yr⁻¹; Buechling et al. 2017), and growing conditions are more limited at the upper (shorter growing season) and lower (drier) treeline (Knight et al. 2014). Among the four species, Douglas-fir radial growth increment is least sensitive to crowding (Buechling et al. 2017), potentially maintaining variability in stand basal area due to early regeneration densities for a longer period of time than in other species.

Models for understanding

Process-based models are often valued for their utility in predicting future landscape trajectories under no-analog conditions (Cuddington et al. 2013, Gustafson 2013). In addition to prediction, their ability to integrate emergent, fine-scale responses to environmental drivers also makes them powerful tools for better understanding ecosystem pattern and process (Grimm et al. 2017, Rastetter 2017). Simulation models can generate hypotheses and new or improved understanding of underlying mechanisms (Seidl 2017), often with relatively low cost and risk (Turner and Gardner 2015). Using study designs such as plausible scenarios and factorial experiments, models allow a greater degree of both control and freedom than might otherwise be logistically or ethically possible (e.g., Carpenter et al. 2015, Hansen et al. 2018). Finally, modeling studies can serve as a benchmark of the historical range of

ecosystem responses to drivers that are expected to change in the future (Seidl et al. 2016b). For example, the results of this study could be used to test whether the relative importance of the abiotic template in influencing stand structural variability increases in scenarios of future interannual climate variability. Models can serve an important complementary role to field-based studies by generating empirically testable hypotheses and facilitating a synthetic approach to understanding complex systems (Jenerette and Shen 2012, Bowman et al. 2015, Cottingham et al. 2017). In the particular context of simulating variability in ecosystems it has to be noted that models are likely underestimating real-world environmental variation. Stand structural variability is likely higher among real stands compared to our simulations, which did not include covariation between high regeneration densities and favorable abiotic conditions (Schoennagel et al. 2003, Turner et al. 2004, Donato et al. 2016, Harvey et al. 2016b, Stevens-Rumann et al. 2018), subsequent disturbances (e.g., insect outbreaks; Antos and Parish 2002), interspecific interactions, and seed supply from neighboring stands.

Variability is important for anticipating future forest landscapes

Variability, an understudied metric (Fraterrigo and Rusak 2008) that characterizes many post-disturbance systems (e.g., Kashian et al. 2005b, Suzuki et al. 2009), has substantial implications for future forests. Assumptions that all stands have the same value of aboveground carbon storage (e.g., Bradford et al. 2008) may be inappropriate with increasing fire activity and therefore increasing extent of young, structurally variable forest (Kashian et al. 2006, 2013). When variability is high, mean estimates of stand structure may be increasingly inaccurate predictors of ecosystem patterns and processes (Cottingham et al.

2000, Fraterrigo and Rusak 2008), particularly if relationships between drivers and responses are nonlinear and interact across scales (Lovett et al. 2005, Peters et al. 2007). Increased forest landscape heterogeneity could also dampen the spread or severity of future disturbances (Bebi et al. 2003, Kulakowski and Veblen 2007, Seidl et al. 2016a).

For forests adapted to high-severity, infrequent fire regimes, understanding causes and patterns of variation in early postfire regeneration appears critically important for anticipating long-term landscape variability. Early postfire regeneration (within the first 10-25 years) affected structural trajectories of four widespread conifer species for decades to centuries in stands across a wide gradient of environmental conditions. Regeneration processes, such as seed supply, dispersal, establishment, and early seedling survival, are often highly sensitive to changes in disturbance regimes and environmental fluctuations (Kipfmüller and Kupfer 2005, Larson and Kipfmüller 2010, Harvey et al. 2016b, Kemp et al. 2016, Hansen et al. 2018, Stevens-Rumann et al. 2018). Early regeneration densities may forecast long-term trajectories in ecosystems that experience periodic high-severity disturbances (Turner et al. 1998), although it may be necessary to consider more than just the first few years of establishment (e.g., Peterson and Pickett 1995, Gill et al. 2017). Ongoing research on the effects of changing climate, disturbance regimes, and other drivers of variation in early postfire regeneration is needed to anticipate future forest landscape patterns.

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Table 1. Early postfire regeneration density and abiotic drivers for simulated stands. The same set of conditions was used for model evaluation and the simulation experiment, except that all stands of a given species were assigned identical soil fertility to control for variation in available field data on soil substrate. Median values indicate the no among-stand variation condition.

Variable (units)	Douglas-fir (n = 34)		Lodgepole pine (n = 70)		Subalpine fir (n = 38)		Engelmann spruce (n = 39)	
	Min- Max	Mean (SE) Median	Min- Max	Mean (SE) Median	Min- Max	Mean (SE) Median	Min- Max	Mean (SE) Median
Time since fire (years)*	-	24 (-) 24	-	24 (-) 24	10-19	14 (0.4) 13	10-19	14 (0.5) 13
<i>Postfire regeneration*</i>								
Density of trees, saplings, and seedlings (stems ha ⁻¹)	14-13,653	2,224 (490) 1,370	33-344,075	21,446 (6,546) 4,050	14-3,154	268 (90) 83	14-11,997	610 (327) 83
<i>Climate†</i>								
Mean annual temperature (°C)	1.1-4.3	2.9 (0.1) 3.0	0.0-2.6	1.2 (0.1) 1.1	-1.2-3.1	1.0 (0.2) 0.7	-1.3-3.1	0.8 (0.2) 0.6
Annual precipitation (mm)	444-787	637 (14) 642	629-1,400	888 (22) 853	741-981	847 (11) 866	741-981	855 (11) 877
Daily global radiation (MJ m ⁻²)	15.3-18.4	16.4 (0.1) 16.2	16.8-19.8	18.5 (0.1) 18.5	16.7-20.3	18.6 (0.2) 18.6	16.7-20.3	18.7 (0.2) 18.8
Daily vapor pressure deficit (kPa)	0.42-0.51	0.45 (0.01) 0.45	0.40-0.43	0.42 (0.00) 0.42	0.38-0.46	0.42 (0.00) 0.41	0.38-0.46	0.42 (0.00) 0.41
<i>Soils</i>								
Effective depth (cm)‡	83-152	102 (3) 106	83-137	114 (3) 106	83-152	111 (5) 86	83-152	106 (4) 86
Sand (%)‡	30-71	50 (1) 48	52-56	54 (0) 54	30-56	48 (1) 53	30-56	48 (1) 53

Table 1, cont.

Variable (units)	Douglas-fir (n = 34)		Lodgepole pine (n = 70)		Subalpine fir (n = 38)		Engelmann spruce (n = 39)	
	Min- Max	Mean (SE) Median	Min- Max	Mean (SE) Median	Min- Max	Mean (SE) Median	Min- Max	Mean (SE) Median
<i>Soils (cont.)</i>								
Silt (%)‡	21-49	33 (1) 33	30-33	32 (0) 33	30-49	35 (1) 32	30-49	35 (1) 32
Clay (%)‡	8-22	17 (1) 19	13-15	14 (0) 14	13-21	17 (1) 15	13-21	17 (1) 15
Substrate§	-	Andesite	-	Rhyolite	-	Andesite	-	Andesite

* Postfire regeneration densities and time since fire from field data (Donato et al. 2016, Harvey et al. 2016b, Turner et al. 2016)

† Climate data from Daymet Version 3 (Thornton et al. 2017), extracted using geographic coordinates of field data* or field-verified forest type (Simard et al. 2012).

‡ Soil depth and texture from CONUS-SOIL (Miller and White 1998), extracted using geographic coordinates of field data* or field-verified forest type (Simard et al. 2012).

§ Soil substrate assigned based on parent material associated with each forest type (Despain 1990, Knight et al. 2014). Substrate was used to derive relative fertility.

Table 2. Factors (abiotic conditions, postfire regeneration density) and levels (among-stand variation, no among-stand variation) for 2-by-2 factorial simulation experiment conducted separately for each of four tree species. Abiotic conditions included climate, soil depth, and soil texture. Stands were simulated either using observed ranges of variation (among-stand variation), or a median condition was assigned to all stands (no among-stand variation). This resulted in the four simulation scenarios named in the table, each of which was replicated 20 times for each tree species.

		Postfire regeneration density	
		Among-stand variation	No among-stand variation
Abiotic conditions	Among-stand variation	<i>All vary</i>	<i>Abiotic varies</i>
	No among-stand variation	<i>Regeneration varies</i>	<i>None vary</i>

Table 3. Comparison of drivers of stand structural variability by species. The relative values, overlap in ranges, intersection point, and final values were compared for CVs in *Abiotic* and *Regeneration varies* scenarios ($n = 20$ replicates of each). All years correspond to time since fire. Relative values of subalpine fir and Engelmann spruce were not compared prior to recruitment of trees > 4 m height in *Abiotic* scenario stands (27 and 28 years since fire, respectively).

Variable (units)	Among-stand density ($n = 20$)				Among-stand basal area ($n = 20$)			
	Douglas-fir	Lodgepole pine	Subalpine fir	Engelmann spruce	Douglas-fir	Lodgepole pine	Subalpine fir	Engelmann spruce
<i>Time since fire = 300 years (mean CV among scenarios)</i>								
All vary CV (%)	45	14	31	27	17	10	23	9
Abiotic CV (%)	45	12	29	28	14	10	23	9
Regeneration CV (%)	10	7	5	7	10	3	3	2
None vary CV (%)	8	2	4	4	5	1	2	2
<i>Intersection point of CV in Abiotic and Regeneration varies scenarios</i>								
Time since fire (years)	175	217	95	153	128	67	124	136
Mean CV (%)	37	17	63	13	23	15	30	12
Abiotic: Mean (SE) density (trees ha ⁻¹)	278 (3)	773 (6)	459 (12)	887 (16)	302 (3)	1,603 (14)	797 (14)	958 (20)
Regeneration: Mean (SE) density (trees ha ⁻¹)	276 (3)	1,020 (7)	272 (11)	938 (21)	292 (3)	2,042 (17)	525 (13)	850 (20)
Abiotic: Mean (SE) basal area (m ² ha ⁻¹)	40.4 (0.2)	43.6 (0.2)	10.9 (0.3)	41.4 (0.1)	37.5 (0.3)	47.0 (0.3)	24.9 (0.5)	39.9 (0.3)
Regeneration: Mean (SE) basal area (m ² ha ⁻¹)	30.1 (0.2)	41.9 (0.2)	6.2 (0.2)	35.9 (0.3)	25.1 (0.2)	41.1 (0.3)	19.1 (0.4)	32.2 (0.3)

Table 3, cont.

Variable (units)	Among-stand density (n = 20)				Among-stand basal area (n = 20)			
	Douglas-fir	Lodgepole pine	Subalpine fir	Engelmann spruce	Douglas-fir	Lodgepole pine	Subalpine fir	Engelmann spruce
<i>Comparison of relative CV ranges in Abiotic and Regeneration varies scenarios</i>								
<i>Regeneration CV > Abiotic CV (years)</i>	24-158	24-187	27-82	28-103	24-106	24-60	27-92	28-125
<i>Regeneration and Abiotic CVs overlap (years)*</i>	159-193	188-272	83-175	104-240	107-300	61-71	93-147	126-146
<i>Abiotic CV > Regeneration CV (years)</i>	194-300	273-300	176-300	241-300	-	72-300	148-300	147-300

* The range of *Regeneration varies* and *Abiotic varies* overlap encompasses the first to last point of overlap, and in some cases includes non-overlapping years.

Figure Legends

Figure 1. Climate envelope for evaluation and simulation experiments, characterized by mean annual precipitation and mean annual temperature (derived from 1980-2015 daily climate data; Thornton et al. 2017) for each species. Each simulated stand is represented by one point within this climate space. Median climate conditions are shown in red. Subalpine fir and Engelmann spruce have the same median climate.

Figure 2. Plot locations (Simard et al. 2012, Donato et al. 2016, Harvey et al. 2016b, Turner et al. 2016) within the Greater Yellowstone Ecosystem used for data on postfire regeneration, climate, and soils to simulate stand development in iLand. Fire years for postfire regeneration plots are indicated with differential shading, and additional climate and soil plots were identified to better encompass the expected range of variability in abiotic conditions for each species. Data sources: ESRI, Tele Atlas, National Atlas of the United States, YNP Spatial Analysis Center, and Monitoring Trends in Burn Severity (MTBS).

Figure 3. (a-h) Trajectories of stand density and basal area over time. All values are for trees > 4 cm diameter at breast height (DBH) to be consistent with the measurements reported in available field data. Density is on a log10 scale. Lines show simulated stand trajectories, and points show field observations, differentiated by data source [research publications (Kashian et al. 2005a, 2005b, Simard et al. 2011, Donato et al. 2013a, Griffin et al. 2013) or FIA Database (USDA Forest Service 2016)].

Figure 4. (a-h) Mean stand density and mean among-stand density CV for the four simulation scenarios (see Table 2) over 300 years of postfire stand development ($n = 20$ replicates of each). All metrics are for trees > 4 m in height. All vertical axes are on a log₁₀ scale to facilitate comparison over time and among simulations.

Figure 5. (a-h) Mean stand basal area and mean among-stand basal area CV for the four simulation scenarios (see Table 2) over 300 years of postfire stand development ($n = 20$ replicates of each). All metrics are for trees > 4 m in height. The vertical axis for CVs (e-h) is on a log₁₀ scale to facilitate comparison over time and among simulations.

Figure 6. (a-h) Ranges of CVs (min to max) across $n = 20$ replicates each of *Abiotic varies* and *Regeneration varies* scenarios. (i-j) Timeline plot for all four species, showing time since fire years when *Regeneration* CVs $>$ *Abiotic* CVs (red), years when *Regeneration* and *Abiotic* CV ranges overlapped (purple), and years when *Abiotic* CVs $>$ *Regeneration* CVs (blue). The range of *Regeneration varies* and *Abiotic varies* overlap encompasses the first to last point of overlap, and in some cases includes non-overlapping years. Points indicate the point of intersection of the mean trajectories for each species. Psme = Douglas-fir, Pico = lodgepole pine, Abl = subalpine fir, and Pien = Engelmann spruce.

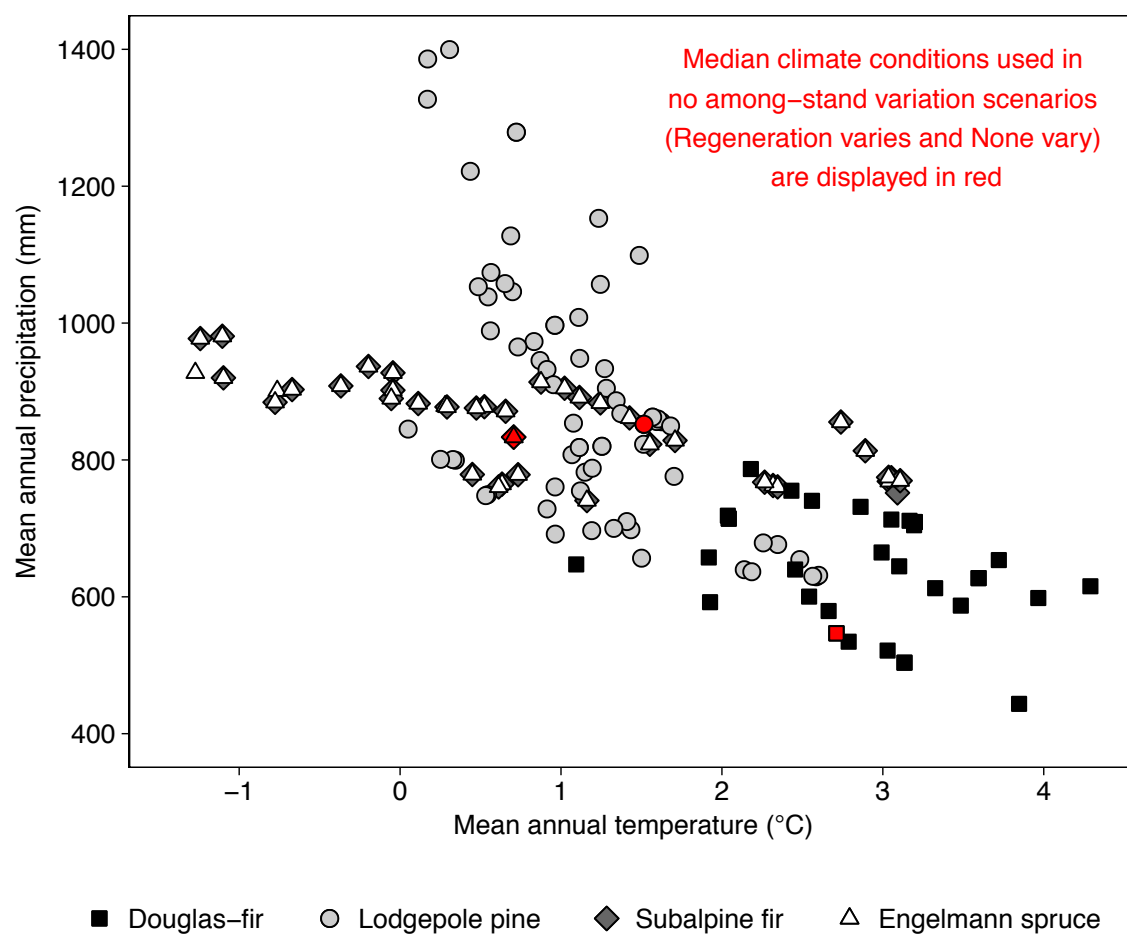


Figure 1

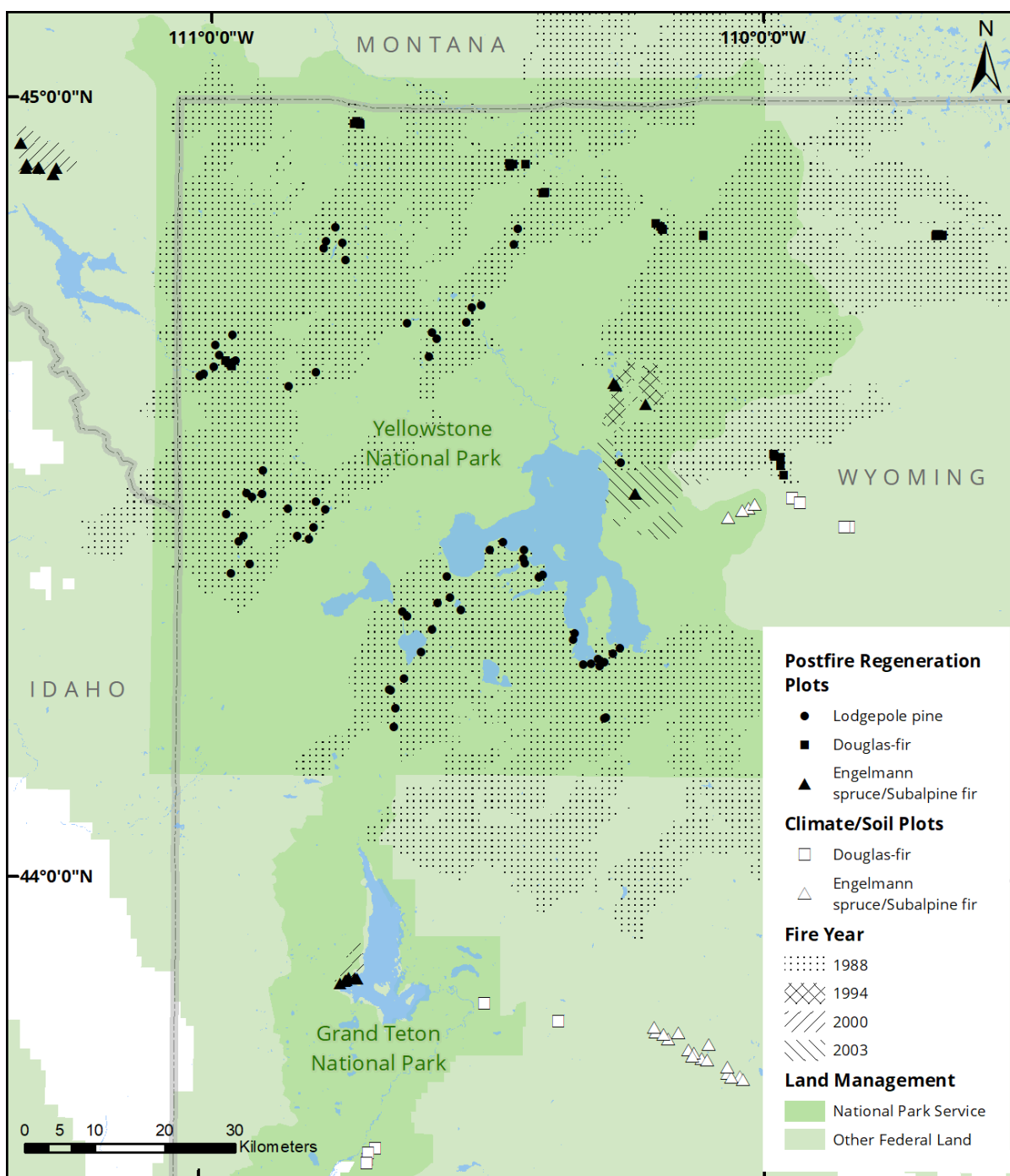


Figure 2

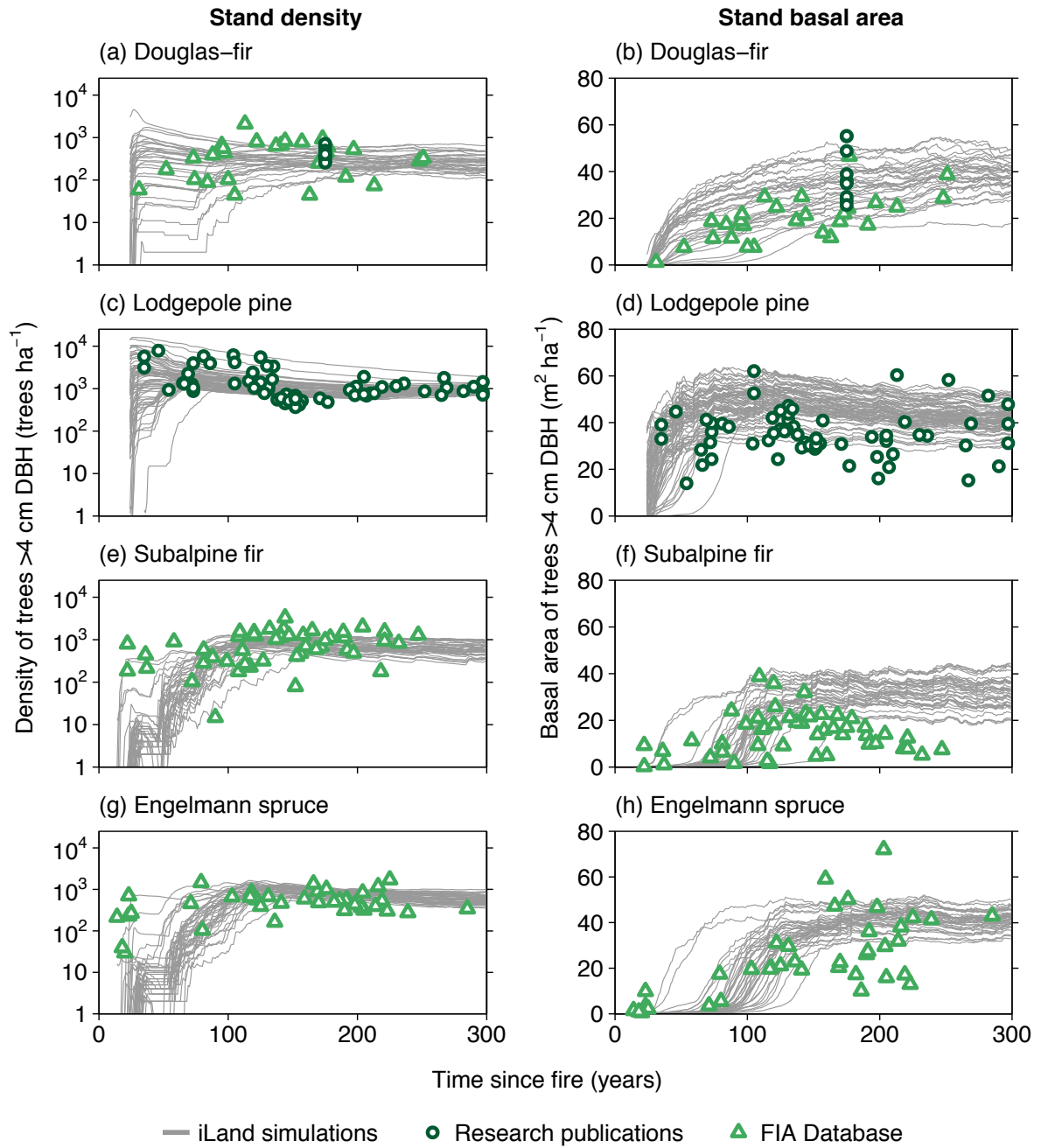


Figure 3

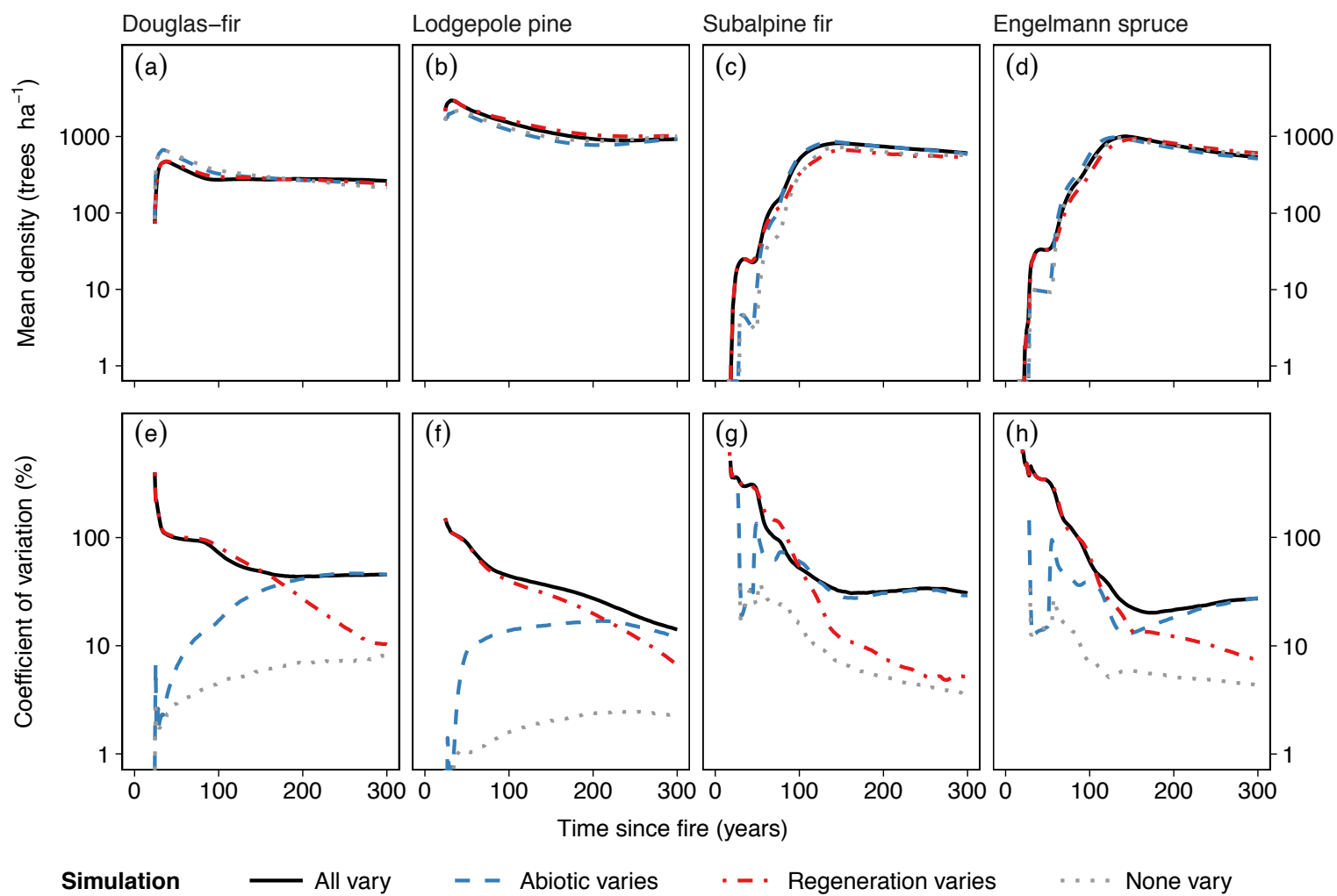


Figure 4

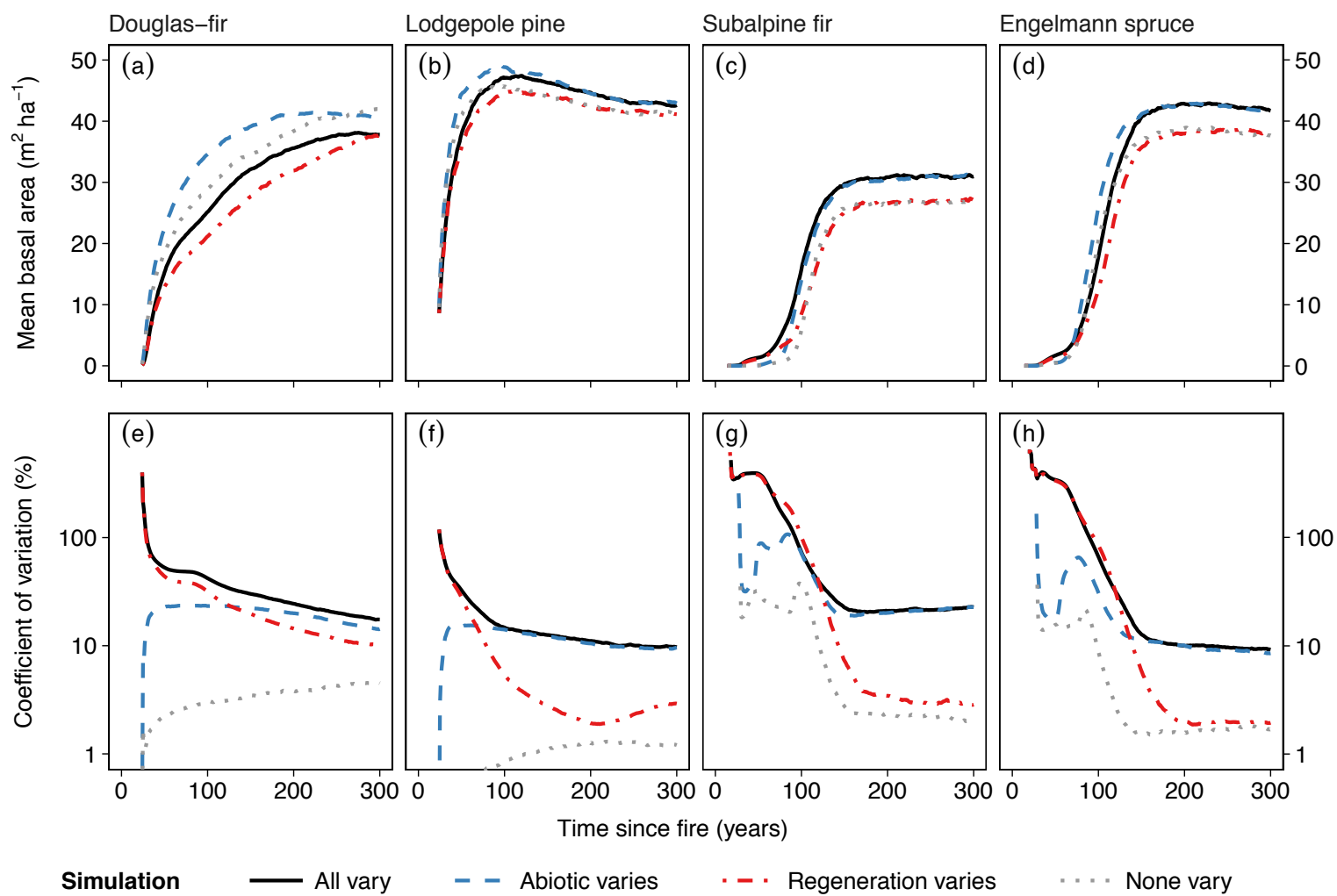


Figure 5

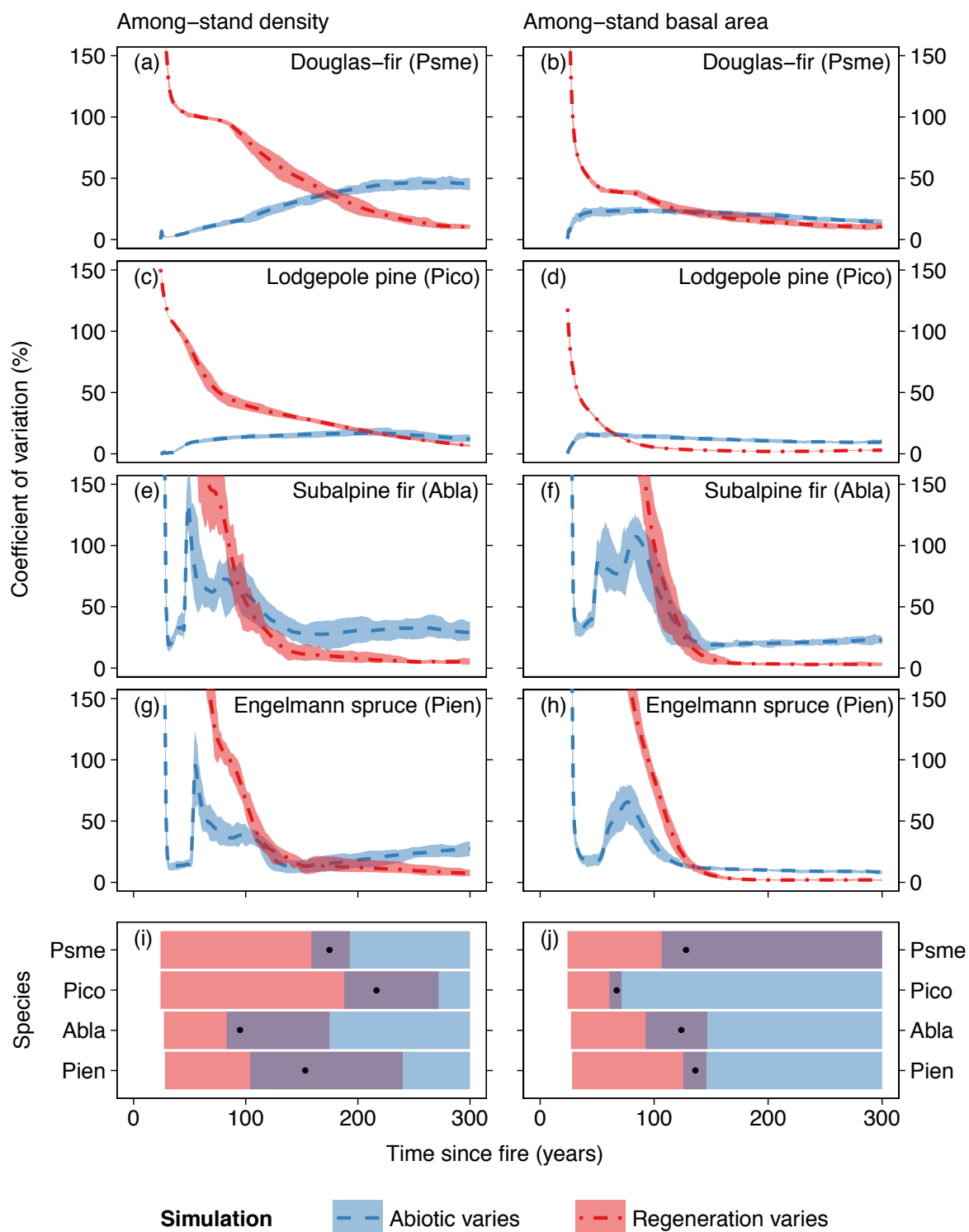


Figure 6

Appendices

Appendix A. Parameters

We parameterized iLand for four widespread conifer species in the Greater Yellowstone Ecosystem (GYE): Lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). The majority of species-specific parameters were sourced from peer-reviewed literature and government reports. A few parameters (e.g., height-to-diameter ratios, aging) were fit or iteratively derived by simulating stand development of initial conditions (see Seidl et al. 2012 and Seidl and Rammer 2018). Species parameters are reported in Table A1. Regional, non-species-specific model parameters for the GYE, such as atmospheric CO₂ concentration, are reported in Table A2. Extensive model documentation and parameter descriptions are available at <http://iland.boku.ac.at/>, and a sensitivity analysis of species parameters was performed by Seidl et al. (2012).

Some lodgepole pine trees produce serotinous cones (closed cones that retain seeds and only open in response to elevated temperatures, such as those experienced during fire), while others only produce cones that are non-serotinous and open at maturity (Tinker et al. 1994). To capture the resulting differences in postfire regeneration, serotinous and non-serotinous lodgepole pine were simulated as two separate “species,” and parameters for serotinous lodgepole pine were derived by Hansen et al. (2018).

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Table A1. Species-specific parameters for conifers in the Greater Yellowstone Ecosystem.

Abla = *Abies lasiocarpa*, Pico = *Pinus contorta* var. *latifolia* (non-serotinous), PicS = *Pinus contorta* var. *latifolia* (serotinous), Pien = *Picea engelmannii*, and Psme = *Pseudotsuga menziesii* var. *glauca*; dim = dimensionless, exp = expression, sdlings = seedlings.

Parameters are fully described in Seidl and Rammer (2018).

Parameter	Unit	Source	Abla	Pico	PicS	Pien	Psme
<i>Tree growth</i>							
Specific leaf area	m ² kg ⁻¹	1–4	4.4	4.6	4.6	5.0	5.8
Leaf turnover	yr ⁻¹	5,6	0.14	0.33	0.33	0.17	0.20
Root turnover	yr ⁻¹	3	0.33	0.33	0.33	0.33	0.33
Height to diameter low a	dim	6–12,71	33.80	38.51	38.51	29.79	44.37
Height to diameter low b	dim	6–12,71	-0.101	-0.126	-0.126	-0.0752	-0.131
Height to diameter high a	dim	6–12,71	169.39	287.99	287.99	188.96	439.47
Height to diameter high b	dim	6–12,71	-0.249	-0.288	-0.288	-0.245	-0.476
Wood density	kg m ⁻³	6	309	380	380	330	450
Form factor	dim[0,1]	13–16	0.466	0.470	0.470	0.469	0.453
<i>Biomass allocation</i>							
Stem wood biomass a	*	17–21	0.04687	0.1401	0.1401	0.2462	0.04510
Stem wood biomass b	*	17–21	2.527	2.136	2.136	2.049	2.634
Stem foliage biomass a	*	19,21–23	0.3894	0.02723	0.02723	0.02860	0.3021
Stem foliage biomass b	*	19,21–23	1.231	1.882	1.882	2.010	1.308
Root biomass a	*	10,24	0.02327	0.021	0.021	0.01135	0.02002
Root biomass b	*	10,24	2.313	2.281	2.281	2.522	2.450
Branch biomass a	*	19,21–23	0.1926	0.01903	0.01903	0.05266	0.2624
Branch biomass b	*	19,21–23	1.571	2.120	2.120	2.060	1.546
<i>Mortality</i>							
Probability of survival to max age (intrinsic mortality)	dim[0,1]	25,71	0.10	0.10	0.10	0.10	0.20
Stress-related mortality	dim	3,71	1.0	1.0	1.0	1.0	1.0
<i>Aging</i>							
Max age	years	26–28,71	300	500	500	600	400
Max height	m	26,27,29	42	41	41	55	57
Aging a	dim	30,71	0.75	0.50	0.50	0.75	0.60
Aging b	dim	30,71	2.50	2.50	2.50	2.50	4.50
<i>Environmental responses</i>							
Vapor pressure deficit response	dim	3	-0.65	-0.65	-0.65	-0.65	-0.65

Table A1, cont.

Parameter	Unit	Source	Abla	Pico	PicS	Pien	Psme
<i>Environmental responses (cont.)</i>							
Min temperature	°C	3,31–34, 71	-4.0	-6.0	-6.0	-6.0	-6.0
Optimum temperature	°C	3,31–34, 71	19.0	17.0	17.0	17.0	17.0
Nitrogen class	dim[1,3]	35,36,71	2.5	1.0	1.0	2.5	1.5
Phenology	int[0,2]	29	0	0	0	0	0
Max canopy conductance	m s ⁻¹	3	0.017	0.017	0.017	0.017	0.017
Min soil water potential	MPa	27,37,38, 71	-1.91	-2.0	-2.0	-1.78	-2.40
Light response	dim[1,5]	27,71	4.5	2.0	2.0	4.0	2.5
Fine root to foliage ratio	dim[0,1]	39,71	0.75	0.75	0.75	0.75	0.75
<i>Seed production and dispersal</i>							
Cone bearing age	years	26,27,29, 40, 71	25	15	15	25	55
Seed year interval	years	26,29, 41–47,71	4	1	1	5	5
Non-seed year fraction	dim[0,1]	26,29, 41–47,71	0.25	0	0	0.1	0.24
Seed mass	mg	29,33,42	13.03	4.1	4.1	3.37	11.31
Germination rate	dim[0,1]	47–52,71	0.229	0.36	0.36	0.114	0.30
Fecundity	sdlings m ⁻²	51,53,71	30.0	115.9	115.9	42.8	43.9
Seed kernel a	m	29,54–58	19	6	6	19	30
Seed kernel b	m	29,54–58	110	160	160	110	200
Seed kernel c	dim[0,1]	29,54–58	0.2	0.05	0.05	0.2	0.2
<i>Establishment</i>							
Min temperature	°C	59	-67	-85	-85	-45	-37
Chill requirement	days	59	60	63	63	49	56
Min growing degree days	degree days	59	198	186	186	74	340
Max growing degree days	degree days	59	5444	3374	3374	1911	3261
Growing degree days base temperature	°C	59	2.6	2.9	2.9	3.1	3.4
Growing degree days before bud burst	degree days	59	119	116	116	145	255
Frost free days	days	59	95	80	80	30	100
Frost tolerance	dim[0,1]	59	0.9	0.9	0.9	0.9	0.5
Min soil water potential	MPa	55,60,61, 71	-2.5	-2.3	-2.3	-2	-7
<i>Sapling growth</i>							
Sapling growth a	dim	6–12, 62–69	0.029	0.05	0.05	0.020	0.036
Sapling growth b	m	6–12,27, 62–69	38	24	24	55	47

Table A1, cont.

Parameter	Unit	Source	Abla	Pico	PicS	Pien	Psme
<i>Sapling growth (cont.)</i>							
Max stress years	years	39,71	2	2	2	2	3
Stress threshold	dim[0,1]	39,71	0.2	0.2	0.2	0.1	0.05
Height to diameter ratio	dim	6,8,11,12	75	72	72	72	88
Reineke's R	saplings ha ⁻¹	6,8,11,12, 39,55,71	350	14.33	550	400	500
Reference ratio	dim[0,1]	71	0.345	0.457	0.457	0.409	0.451
<i>Serotiny</i>							
Serotiny formula	exp	8			(x,20,0, 80,1)		
Serotiny fecundity	dim	8			30		
<i>Crown parameters for light influence patterns</i>							
Crown shape coefficient	dim	70	0.2530	0.2700	0.2700	0.2615	0.3015
Max crown radius a	m	70	0.9778	1.1194	1.1194	1.0486	1.3817
Max crown radius b	m	70	2.2195	2.7325	2.7325	2.4760	3.6825
Relative crown height	dim[0,1]	27,39,70	0.5450	0.3065	0.3065	0.4190	0.4356

* Used in allometric equation to calculate biomass (kg) from diameter at breast height (cm).

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Table A2. Regional model parameters for the Greater Yellowstone Ecosystem, which apply to all stands in the simulation. Parameters from Seidl et al. (2012) were used or modified for this study. Additional regional parameters were set to default values per Seidl and Rammer (2018).

Parameter	Units	Value
Light extinction coefficient	dim	0.5
Potential light utilization efficiency	g C MJ ⁻¹	2.9
Boundary layer conductance	mm s ⁻¹	0.15
Temperature delay time constant	days	6.0
Base CO ₂ concentration	ppm	330
Latitude	°N	44.5

Appendix B. Model evaluation

We evaluated iLand's ability to simulate stand structural development under historical climatic conditions in the Greater Yellowstone Ecosystem (GYE) in three stages: Evaluation of monospecific stands, evaluation of mixed-species stands, and comparison with the forest growth model Forest Vegetation Simulator (FVS; Dixon 2002). Evaluations were designed to assess how well iLand characterized (1) single-species stand structural trajectories and variability over time, (2) successional trajectories, species composition, and stand structure in late-seral stages in different forest types, and (3) responses to variation in initial stem densities and environmental conditions. Comparison of stand development with FVS allowed us to evaluate iLand against the simulator used most widely by federal forest managers in the western United States.

(1) Single-species evaluation

We first evaluated simulated structural trajectories and variability over time for monospecific stands based on stand density, basal area, quadratic mean diameter (QMD), and mean height for each of the four dominant conifer species. Methods and results for stand density and basal area are described in the main body of the paper. Simulated QMDs and heights fell within observed ranges of field data (Kashian et al. 2005a, 2013, Simard et al. 2011, Donato et al. 2013a, Griffin et al. 2013, USDA Forest Service 2016), and variation among stands was maintained over time (Figure B1).

(2) Mixed-species evaluation

We next evaluated iLand's ability to achieve expected late-seral stand structure and species composition after 300 years of succession in three distinct, widespread forest types in the GYE: (1) Low-elevation Douglas-fir, (2) mid-elevation lodgepole pine, and (3) high-elevation spruce-fir. Geographic locations for each forest type were determined by extracting random points > 1 km apart from a map of Yellowstone National Park (YNP) pre-1988 cover types (Despain 1990, provided by YNP Spatial Analysis Center). To minimize overlap between climatic conditions of the three forest types, high-elevation Douglas-fir, low-elevation spruce-fir, and extreme high- and low-elevation lodgepole pine points were removed (elevations from 10-m Digital Elevation Model provided by YNP Spatial Analysis Center). From this dataset, 10 points were randomly sampled from each forest type (Table B1) and used to derive historical climatic (Daymet Version 3; Thornton et al. 2017) and edaphic (CONUS-SOIL; Miller and White 1998) conditions for simulated stands (see Figure B2 for climate envelope). Relative soil fertility was assigned based on soil parent material associated with each forest type (andesite for Douglas-fir and spruce-fir, rhyolite for lodgepole pine; Despain 1990, Knight et al. 2014).

For each forest type, 10 1-ha stands were simulated for 300 years (climate year drawn randomly with replacement, no disturbance) along an elevation transect, starting from bare ground and allowing seed inputs from two, opposite sides (Figure B3). Seed availability differed by forest type based on tree species composition (Table B1), and once mature trees had established, simulated stands could also serve as seed sources for each other. Because seed inputs were affected by stochastic processes (e.g., probability of mast year) and we were

interested in capturing a wide range of stand structures, simulations were replicated three times for a total of $n = 30$ per forest type.

Simulated stand trajectories of tree density, basal area, and importance value (IV, species proportion of density + species proportion of basal area, potential range from zero to two) were consistent with expectations of succession over time for the studied forest types (Figure B4). Early pulses of lodgepole pine regeneration occurred in both Douglas-fir and spruce-fir forests (Figure B4a,c), but after 300 years of stand development, forest types were dominated by expected species (Figure B4g,i). Subalpine fir IV declined in older spruce-fir stands (Figure B4i), which is consistent with expected increasing spruce dominance (Baker 2009).

Simulated mature (300-year-old) stand structure and dominant species composition overlapped with observed ranges in field data (Figures B5-B7; Binkley et al. 2003, Kashian et al. 2005b, Donato et al. 2013b). However, simulated stem densities did not reach the highest values recorded in field data, and median simulated densities were lower than median observed densities (Figures B5-B7a). These discrepancies likely reflect the subsetting of simulated forest types by elevation (e.g., low-elevation Douglas-fir stands are more dry than mesic) and the lack of fire-induced regeneration of serotinous lodgepole pine. Basal areas and dominance of species were mostly consistent with field observations (Figures B5-B7b-c).

(3) Model comparison with FVS

We evaluated iLand's ability to respond appropriately to variation in initial stem densities and environmental conditions by comparison with the Forest Vegetation Simulator

(FVS; Dixon 2002), a widely used semi-distance-independent individual-tree growth and yield model parameterized for the GYE (Teton Variant; Keyser and Dixon 2008). In FVS, stand level variables such as elevation, slope, and aspect incorporate environmental variation among sites and affect tree growth. We simulated single-species stand development of the same lodgepole pine ($n = 70$) and Douglas-fir ($n = 34$) stands (starting at 24 years postfire) in both iLand and FVS for 300 years without disturbance under historical climate conditions. Initial conditions and simulation in iLand followed the methods for (1) single-species evaluation, and initial conditions for FVS (densities, tree sizes, stand environmental variables) were derived from the same field data. We used empirically-derived parameters from two studies that successfully evaluated and applied FVS for these two species in the GYE (Donato et al. 2013b, Seidl et al. 2016) to adjust tree growth, mortality, and infilling in FVS.

Stand densities and basal areas for the same stands simulated in iLand versus FVS were compared at three time periods (74, 124, and 224 years postfire; Figures B8 and B9). Spearman's rank order correlation was used to compare stands modeled with iLand and FVS because assumptions of normality and linearity were not met. After 50 years of simulation (74 years postfire), iLand and FVS represented lodgepole pine stand densities and Douglas-fir stand densities and basal areas similarly across a wide range of initial densities and environmental conditions ($r_s = 0.71, 0.95$, and 0.72 , respectively, all $p < 0.001$), but iLand and FVS-simulated lodgepole pine basal areas were only weakly correlated ($r_s = 0.29$, $p < 0.05$). In both cases the strength of correlation between iLand and FVS for the same stands decreased with stand age (Figures B8 and B9).

Simulated iLand and FVS stand trajectories for density and basal area were compared over 300 years with each other and with field observations (combined research publication and FIA data from single-species evaluation; Figure B10). Although the ranges overlapped for much of earlier (< 150 years) stand development, development trajectories differed over time. FVS median stand densities were mostly higher and median basal areas appeared to more closely follow a logistic (Douglas-fir) or logarithmic (lodgepole pine) growth curve than in iLand. During the first 150 years of simulation, both models maintained variation in stand density and basal area and encompassed many of the field observations. Later in stand development, FVS simulations converged, particularly for basal area, which is consistent with intended model behavior to approach a maximum stand density index in the absence of disturbance (Crookston and Dixon 2005). However, iLand simulations continued to capture the variability observed in field data for late-seral stands.

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Table B1. Elevation ranges and seed source species composition for each forest type. All species were included as potential seed sources in all forest types (minimum value = 0.01). Species composition was calculated from trees greater than breast height in reference field data. Abl = *Abies lasiocarpa* (subalpine fir), Pico = *Pinus contorta* var. *latifolia* (lodgepole pine), Pien = *Picea engelmannii* (Engelmann spruce), and Psme = *Pseudotsuga menziesii* var. *glauca* (Douglas-fir).

Forest type	Elevation range (m)	Seed source species composition				Reference for seed source species composition
		Abla	Pico	Pien	Psme	
Douglas-fir	1,993-2,275	0.06	0.16	0.02	0.76	Donato et al. 2013, 150-200-year-old Douglas-fir forest
Lodgepole pine	2,196-2,573	0.03	0.90	0.03	0.04	Kashian et al. 2005b, 250-358-year-old stands in a lodgepole pine chronosequence
Spruce-fir	2,427-2,774	0.52	0.03	0.44	0.01	Binkley et al. 2003, 200-450-year-old spruce-fir forest

Figure Legends

Figure B1. (a-h) Single-species stand trajectories in quadratic mean diameter (QMD) and mean stand height over time. All values are for trees > 4 m in height. Lines show simulated stand trajectories, and field observation points are differentiated by data source (research publications or FIA Database).

Figure B2. Climate envelope for mixed-species evaluation, characterized by mean annual precipitation and mean annual temperature for each forest type. Each simulated stand is represented by one point within this climate space.

Figure B3. Simulation layout for a single forest type. Each forest type was simulated separately. Stands (1-ha, $n = 10$ per simulation) were arranged from low to high elevation, with seed inputs from both adjacent sides. Seed availability differed by forest type (Table B1), and once mature trees had established, simulated stands could also serve as seed sources for each other.

Figure B4. Mean ($n = 30$) stand structural trajectories (based on trees > breast height) for three forest type transects [Douglas-fir (a, d, g), lodgepole pine (b, e, h), and spruce-fir (c, f, i)], starting from bare ground with multispecies seed inputs. Importance values (g-i) were calculated for each species (maximum value = 2). Abia = *Abies lasiocarpa*, Pico = *Pinus contorta* var. *latifolia*, Pien = *Picea engelmannii*, and Psme = *Pseudotsuga menziesii* var. *glauca*.

Figure B5. Boxplot comparison of forest structure and species composition in simulated mature Douglas-fir stands (300 years old, $n = 30$) with lower-montane, mature Douglas-fir dominated stands in the GYE on mesic ($n = 23$) and dry ($n = 32$) topographic positions (Donato et al. 2013b). Total (all species) stand densities (a), total basal areas (b), and Douglas-fir dominance as proportion of tree density (c) were calculated for trees > 15 cm DBH to be consistent with field observations. Bold lines show the median value, boxes show the interquartile range (IQR), and whiskers extend $1.5 \times$ IQR or to the most extreme data point (whichever is closest to the median). Psme = *Pseudotsuga menziesii* var. *glauca*, prop = proportion.

Figure B6. Boxplot comparison of forest structure and species composition in simulated mature lodgepole pine stands (300 years old, $n = 30$) with mature stands in a lodgepole pine chronosequence in the GYE (250-358-year-old stands, $n = 12$; Kashian et al. 2005b). Total (all species) stand densities (a), total basal areas (b), and lodgepole pine dominance as proportion of tree density (c) were calculated for trees > 4 cm DBH to be consistent with field observations. Bold lines show the median value, boxes show the interquartile range (IQR), and whiskers extend $1.5 \times$ IQR or to the most extreme data point (whichever is closest to the median). Pico = *Pinus contorta* var. *latifolia*, prop = proportion.

Figure B7. Boxplot comparison of forest structure and species composition in simulated mature spruce-fir stands (300 years old, $n = 30$) with old growth spruce-fir stands in Colorado (200-450-year-old stands, $n = 18$; Binkley et al. 2003). Total (all species) stand

densities (a), total basal areas (b), and subalpine fir (c) and Engelmann spruce (d) dominance as proportion of tree density were calculated for trees > breast height to be consistent with field observations. Bold lines show the median value, boxes show the interquartile range (IQR), and whiskers extend 1.5 x IQR or to the most extreme data point (whichever is closest to the median). Abl = *Abies lasiocarpa*, Pien = *Picea engelmannii*, prop = proportion.

Figure B8. Comparison of densities (a-c) and basal areas (d-f) for the same Douglas-fir stands ($n = 34$, each stand = 1 point) simulated in iLand and FVS at three time periods: 74, 124, and 224 years postfire. Stand structure was calculated from trees > 4 m in height. Stand density is on a log10 scale, and a 1:1 line is shown for comparison on each plot. Spearman's rank correlation coefficient and two-tailed p-values are noted on each plot. * $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, *** $p < 0.001$, ns = not significant at $\alpha = 0.05$.

Figure B9. Comparison of densities (a-c) and basal areas (d-f) for the same lodgepole pine stands ($n = 70$, each stand = 1 point) simulated in iLand versus FVS at three time periods: 74, 124, and 224 years postfire. Stand structure was calculated from trees > 4 m in height. Stand density is on a log10 scale, and a 1:1 line is shown for comparison on each plot. Spearman's rank correlation coefficient and two-tailed p-values are noted on each plot. * $0.01 < p < 0.05$, ** $0.001 < p < 0.01$, *** $p < 0.001$, ns = not significant at $\alpha = 0.05$.

Figure B10. Stand trajectories in density (a, c) and basal area (b, d) for lodgepole pine ($n = 70$) and Douglas-fir ($n = 34$) stands simulated with iLand (red shading, solid line) and FVS

(blue shading, dotted line) over time, compared to field observations. All values are for trees > 4 cm diameter at breast height (DBH) to be consistent with the measurements reported in available field data. Density is on a log10 scale. Simulated medians (lines), interquartile ranges (IQR, intermediate shading), and ranges (minimum to maximum values, light shading) are shown.

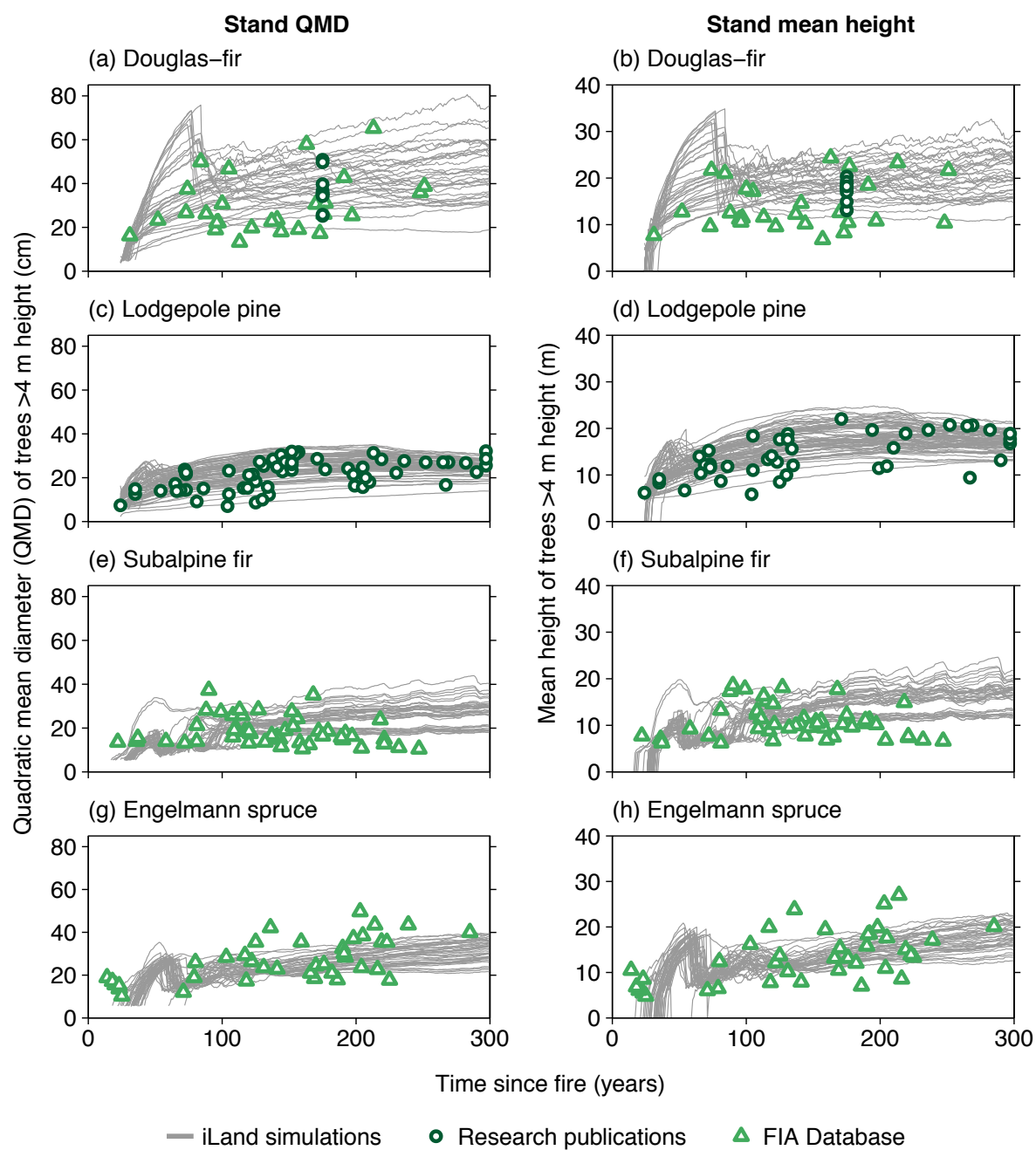
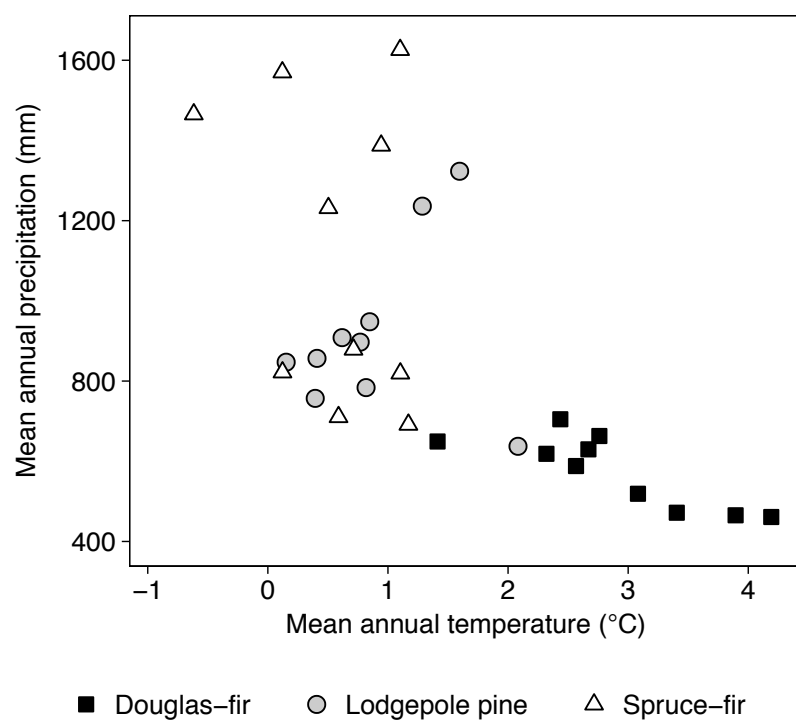
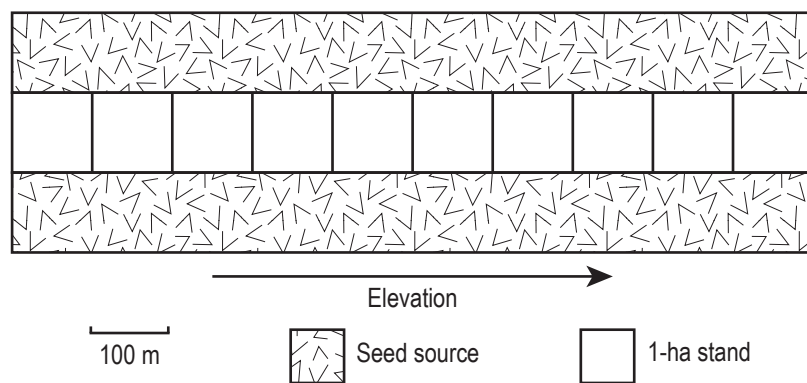


Figure B1

**Figure B2**

**Figure B3**

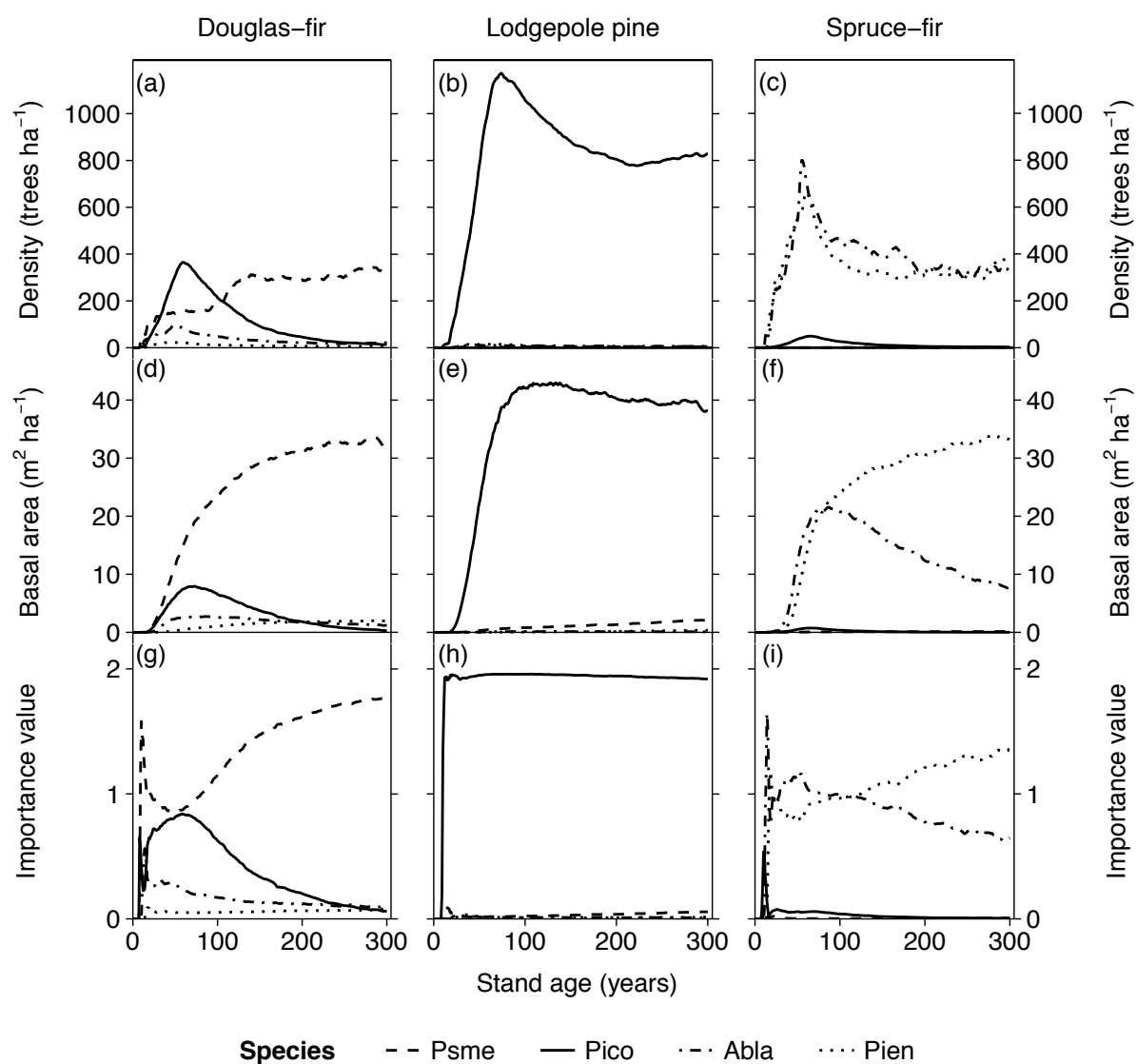


Figure B4

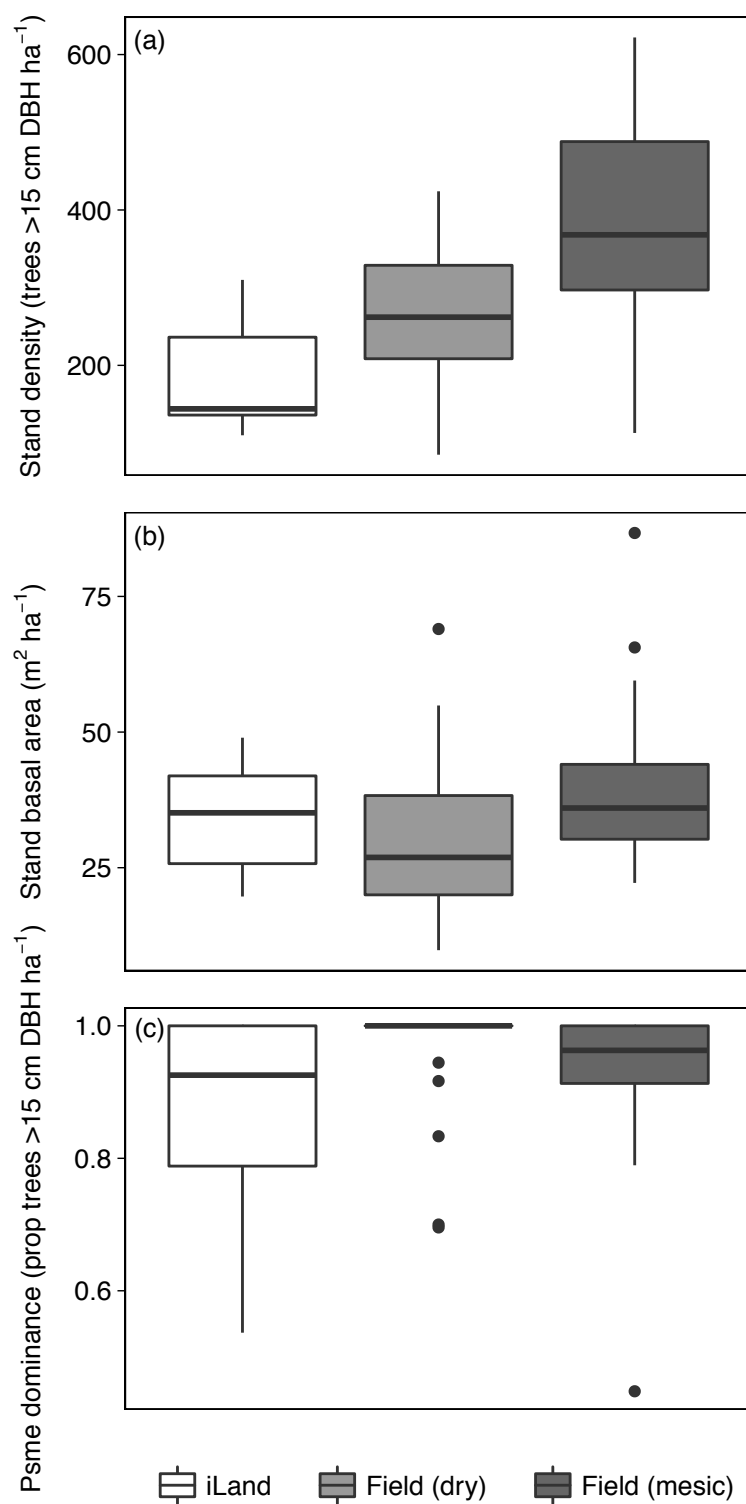
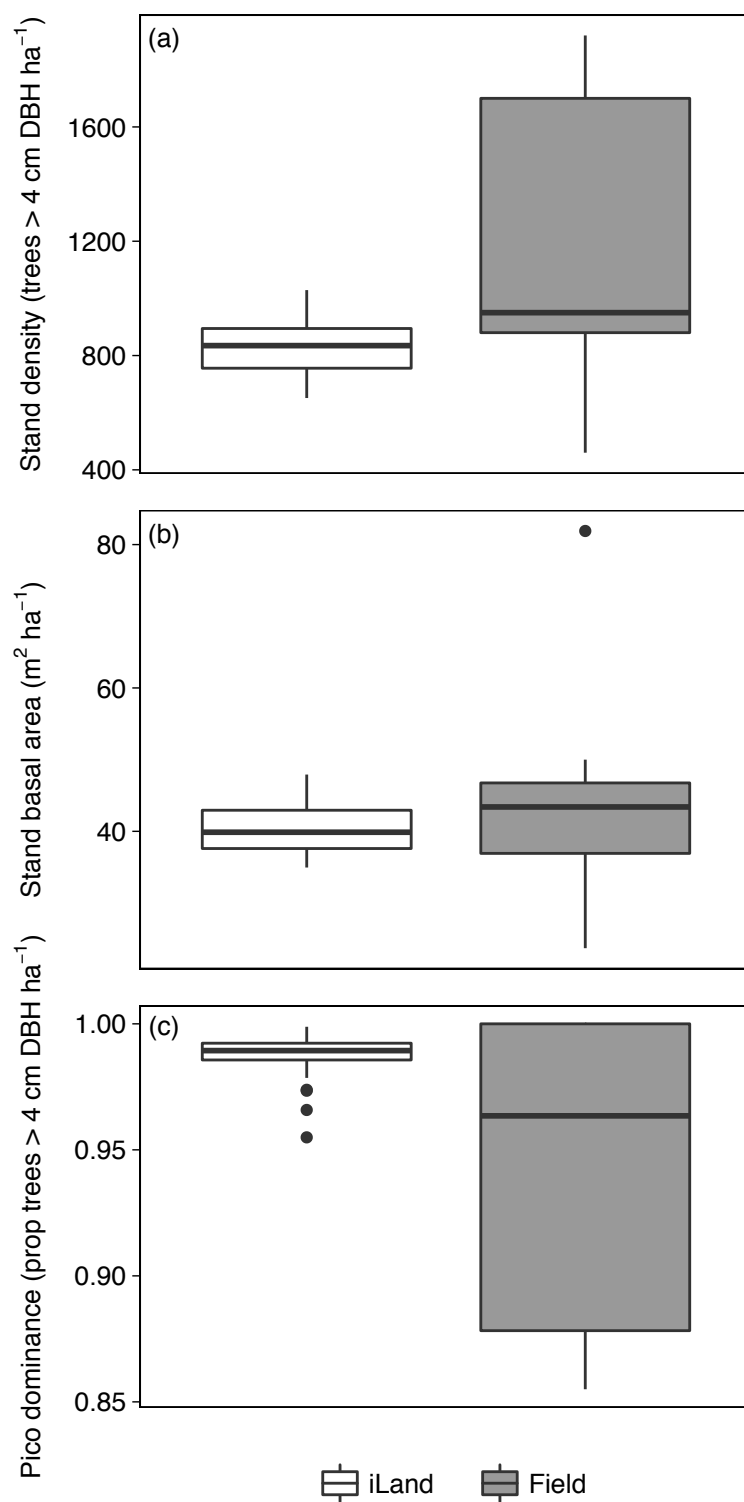
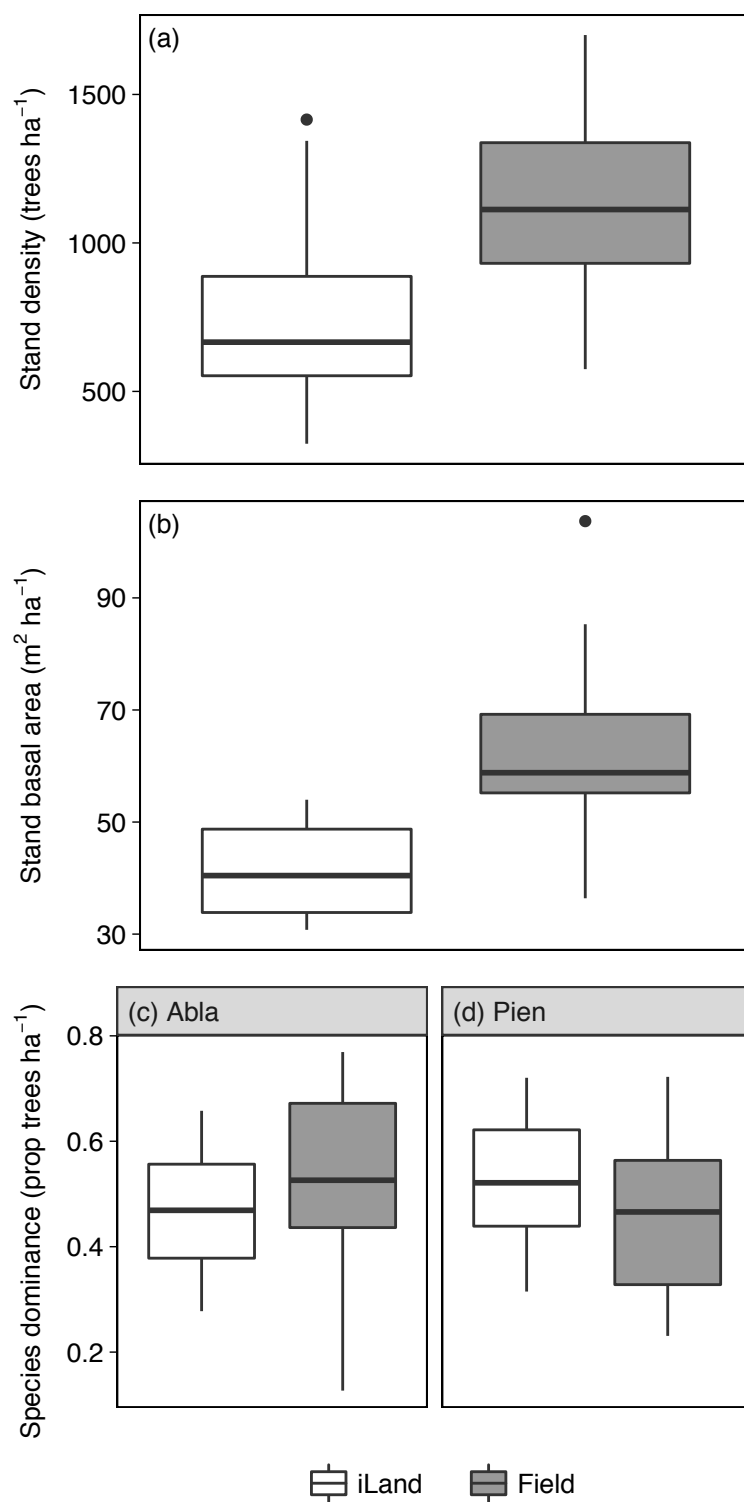


Figure B5

**Figure B6**

**Figure B7**

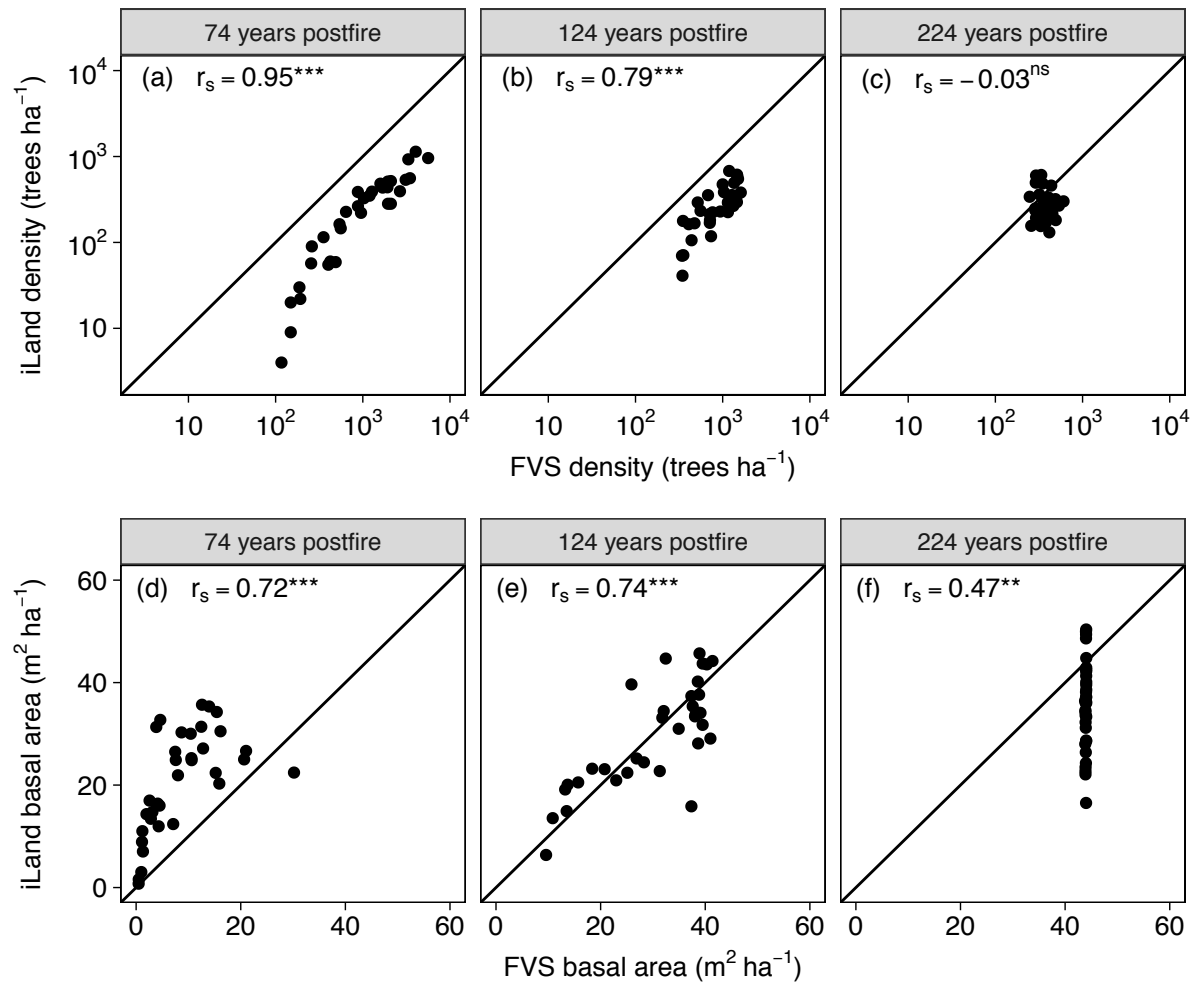


Figure B8

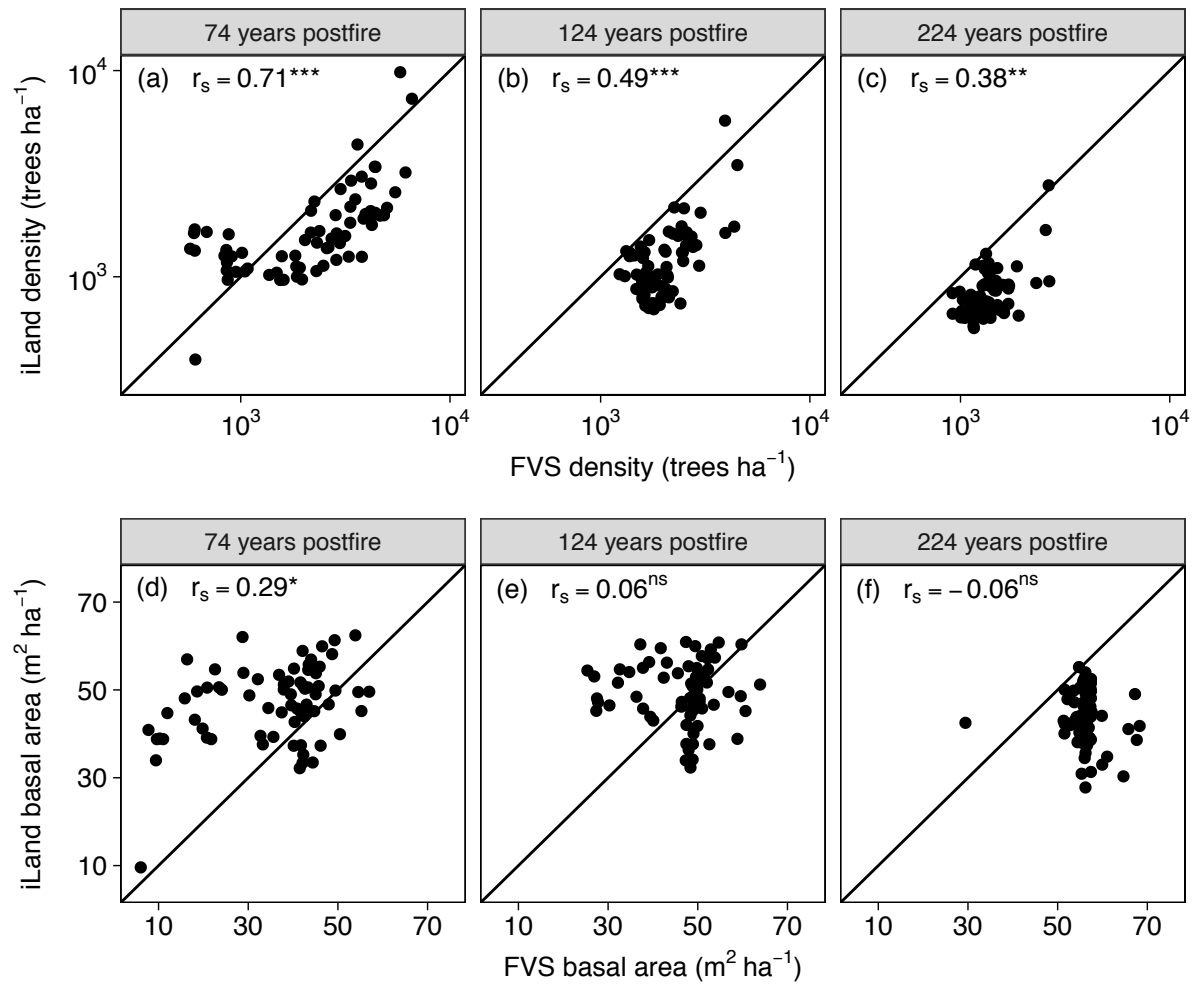


Figure B9

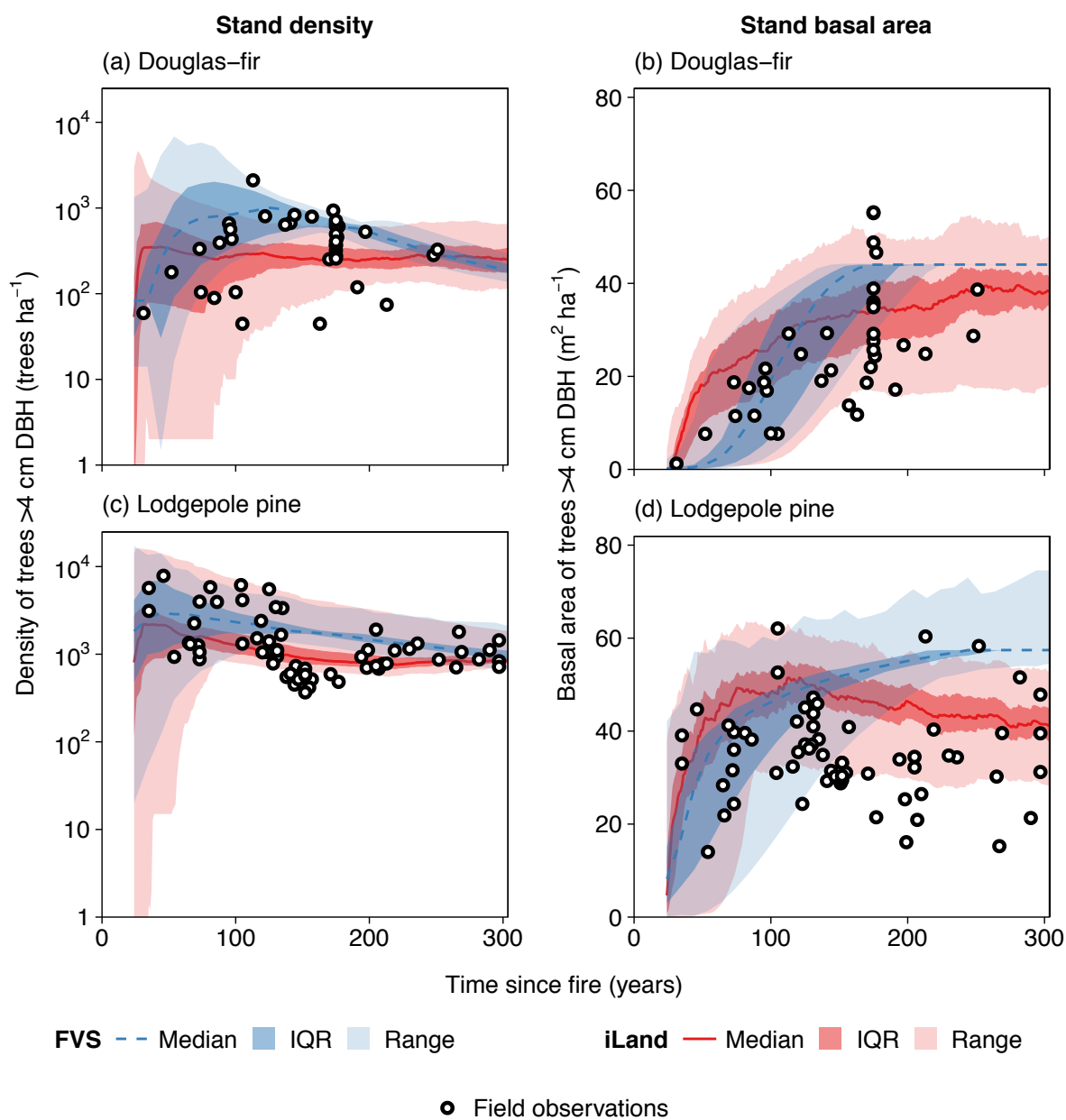


Figure B10